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Photosystem II Tolerance to Excess Zinc Exposure and High Light Stress in *Salvia sclarea* L.

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Abstract: High light (HL) intensity has a substantial impact on light energy flow and partitioning within photosynthetic apparatus. To realize the impact of HL intensity on zinc (Zn) tolerance mechanisms in clary sage (*Salvia sclarea* L., Lamiaceae) plants, we examined the effect of the altered chlorophyll and nutrient uptake under excess Zn supply on the response mechanism of photosystem II (PSII) photochemistry. Eight-week-old clary sage plants were treated with 5 μM Zn (control) or 900 μM Zn in Hoagland nutrient solution. Leaf elemental analysis for Zn, Mn, Mg, and Fe was performed by inductively coupled plasma mass spectrometry (ICP-MS), whereas PSII functioning under HL was evaluated by chlorophyll fluorescence imaging analysis. Exposure of *S. sclarea* plants to 900 μM Zn increased leaf Zn accumulation and decreased leaf Mg and chlorophyll. The decreased non-photochemical quenching (NPQ) provided evidence of the photoprotection offered by the smaller light-harvesting antennae due to the reduced chlorophyll. The increased Mn after Zn exposure corresponded with higher efficiency of the oxygen-evolving complex (OEC) that was significantly correlated with the maximum efficiency of photosystem II (PSII) photochemistry (Fv/Fm). An increased electron transport rate (ETR) coincided with increased leaf Fe, which is known to play a vital role in the enzymes engaged in ETR. The decreased (32%) NPQ after an 8-day exposure to Zn caused an increased (10%) quantum yield of non-regulated energy loss in PSII (Φ_{NO}), indicative of an increased singlet oxygen ($^1O_2$) production. It is suggested that the decreased NPQ induced acclimation responses of clary sage plants to HL and excess Zn by increasing $^1O_2$ production. The reduced (18%) excess excitation energy (EXC) at PSII and the increased (24%) quantum yield of PSII photochemistry (Φ_{PSII}) and ETR indicated improved photosynthetic efficiency under excess Zn and HL intensity. Therefore, the exposure of medicinal plants to excess Zn not only boosts their photosynthetic efficiency, enhancing crop yields, but can also improve Fe and Zn content, ameliorating the human health deficiency of these two essential micronutrients.

Keywords: chlorophyll fluorescence imaging; non-photochemical quenching; chlorophyll content; PSII efficiency; photoprotection; excess excitation energy; electron transport rate; light stress; singlet oxygen; quantum yield of PSII photochemistry

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1. Introduction

Zinc (Zn), a vital micronutrient for plant growth and expansion, exists in plant cells in an oxidized state as Zn^{2+} [1–3]. This divalent cation is indispensable for regular cell

metabolism and fostering robust plant growth [4–8]. Its pivotal role encompasses various critical cellular functions, including the maintenance of structural integrity within diverse cell organelles [9–15]. Zinc acts as a cofactor for numerous enzymes, influencing diverse physiological processes like carbohydrate and lipid metabolism, nucleic acid processing, gene expression, protein synthesis, enzyme activation, and reproductive development [4,16]. Roughly 9% of proteins rely on Zn as a metallic cofactor, whereas it also serves as a structural element in DNA-binding regulatory proteins [17]. Moreover, Zn is integral to various proteins participating in essential biological functions, like transcription, translation, photosynthesis, and the regulation of reactive oxygen species (ROS) [2,8,18]. Additionally, Zn cations and Zn complexes possess antimicrobial and antioxidant properties [19].

Zinc deficiency, prevalent in many agricultural soils [20], significantly hampers plant growth and development, posing a global challenge [4]. To enhance crop yield and nutritional value, ensuring an adequate supply of Zn is recommended [21]. Typically, tissues and organs maintain Zn concentrations of around 50 μg g^{-1} DW, whereas cellular levels range between 100 μM and 500 μM [22]. These levels reflect the widely observed Zn requirements and the regulatory mechanisms maintaining balance [22].

Nevertheless, excessive Zn in the soil can reach concentrations that are harmful, even lethal, for most plants [23], posing a serious threat to global agricultural output [24,25]. When plants are exposed to such conditions, they store excess Zn in their tissues, reaching concentrations that are toxic (>300 μg g^{-1}), which can lead to physiological disturbances and growth retardation [26]. Elevated Zn levels in the environment disrupt crucial metabolic processes, impede the absorption of essential elements, trigger reactive oxygen species (ROS) production, and induce toxicity [27–29]. High Zn concentrations can result in decreased photosynthesis and plant growth, causing leaf discoloration, reduced chlorophyll, necrosis, and hindering various metabolic pathways [9,23,27,30,31]. The adverse impact of excess Zn on photosynthesis has been associated with the generation of ROS, like singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2), superoxide anions ($O_2^{\bullet-}$), and hydroxyl radicals (OH^-), that lead to lipid peroxidation, damaging the cellular membranes [6,16,32–34].

Light is vital for photosynthesis; however, an excessive amount can pose potential harm [35]. Light reactions of photosynthesis include the harvesting of photons by pigments associated with the antennae photosynthetic complexes as the first step, and subsequently, the transfer of the resulting excitation energy to the reaction centers, where it is used to induce charge separation [36,37]. Surplus photons increase the levels of singlet chlorophyll (^{1}Chl*) molecules, thereby increasing the possibility of forming triplet chlorophylls (^{3}Chl*) that react with molecular oxygen (O_2) to form $^1O_2$ [34–37]. Under conditions of low light (LL), most of the absorbed photons by the photosynthetic pigments trigger charge separation in the reaction centers (RCs) of both photosystem I (PSI) and photosystem II (PSII) [34,35]. Conversely, under high light (HL), excess absorbed photons can generate harmful compounds capable of damaging the photosynthetic machinery [38,39] and cause photoinhibition of PSII, which restricts plant growth [40,41]. However, all photosynthetic organisms have evolved an array of photoprotective mechanisms, and the most important mechanism that is rapidly inducible, known as nonphotochemical quenching (NPQ), dissipates a significant portion of excess absorbed light energy as heat, regulating the electron transport rate (ETR) which is disrupted under HL stress conditions [34,42].

The measurement of chlorophyll *a* fluorescence has been widely utilized to assess photosynthetic function, specifically the function of PSII [43–45]. The light energy absorbed by the pigment molecules can be employed for photochemistry or dissipated through various other pathways [46–49]. The portion of absorbed light energy utilized for photochemistry is pivotal for plant productivity [50]. Unused energy, which is not utilized for photochemistry or dissipated as heat, can lead to ROS creation, such as $^1O_2$, $O_2^{\bullet-}$, and H_2O_2 [34,51–54]. To prevent ROS formation and photoinhibition, the absorbed light energy by the antennae must maintain a balance in electron transport from PSII to PSI [55,56]. ROS are partly reduced or excited forms of O_2 that play essential functions in plant cells, implicated in both oxidative damage and signaling and qualified to regulate stress responses and

plant development [34,57–60], involving gene expression [61–63] and various metabolic pathways [64,65].

Plants are the main source of Zn in human nutrition, and human Zn deficiency results in over 400,000 deaths yearly [8]. Several methods have been used to increase the quantity of Zn in nutritive systems [8]. Agronomic farming practices through fertilizers or foliar sprays employ biofortification to enhance Zn bioavailability and uptake in plants [66–69]. Zn application, in cereal-growing regions of arid countries, has become gradually common in order to improve Zn in the grain and yields [70–72]. *Salvia sclarea*, known as clary sage, is a plant species that can accumulate and tolerate high Zn concentrations in its leaves, also increasing other essential elements under excess Zn, which results in improved activities of PSI and PSII [14,73]. This aromatic plant is being used in the pharmaceutical and food industry [74] and is suitable to be used for the phytoextraction and/or phytostabilization of soils contaminated with Zn [2,14,75].

Zinc is an essential micronutrient for plants, whereas light is essential for photosynthesis. However, too much of a good thing is bad. Excess Zn in leaf tissues negatively affects photosynthesis through Zn-induced oxidative damage to membranes [3,6,25], and excess photons cause photoinhibition that limits plant growth [39,40,50]. *Salvia sclarea* plants have been found to possess an adaptive strategy for excess Zn, with photosystem I (PSI) and photosystem II (PSII) activities stimulated under LL conditions [3,14]. However, the response of *Salvia sclarea* PSII photochemistry under HL and excess Zn has not been examined. Thus, in the present work, we grow, in hydroponic culture, *Salvia sclarea* plants with excess Zn supply to evaluate the role of excess Zn as a photosynthetic stimulant in crops growing in HL environments. We also evaluated any enhancement of Zn bioavailability and uptake in plants that could be used to increase the amount of bioavailable Zn in nutritive systems.

2. Materials and Methods

2.1. Plant Material and Growth Conditions

Clary sage (*Salvia sclarea* L.) seeds were kindly provided by Bio Cultures Ltd. (Karlovo, Bulgaria). After surface sterilization, the seeds germinated on soil in a growth room [3]. Four-week *S. sclarea* seedlings were transferred in a hydroponic system for another four-week period in a nonstop aerated nutrient solution [3] which was entirely renewed every 3 days [75,76]. *S. sclarea* plants grew in a 14/10 h day/night photoperiod, with a relative humidity of 55 ± 5/65 ± 5% day/night, and 24 ± 1/20 ± 1 °C day/night temperature [2].

2.2. Zinc Treatments

When the clary sage plants were eight weeks old, they were treated with an excess Zn supply (900 μM Zn as $ZnSO_4$), or with the Hoagland nutrient solution without an additional Zn supply (5 μM Zn, control). The concentration of 900 μM Zn was chosen to be the same with that previously used to evaluate the PSII response mechanism of clary sage to excess Zn exposure under LL [3]. All treatments were performed with three plants and three independent biological replicates.

2.3. Elemental Content Determination by Inductively Coupled Plasma Mass Spectrometry (ICP-MS)

For elemental content analysis, clary sage leaves were harvested, washed, dried at 65 °C, and then processed as described previously [77]. Elemental content analysis was performed by the inductively coupled plasma mass spectrometry (ICP-MS), model ELAN DRC II (PerkinElmer Sciex, Toronto, ON, Canada) [78], for Zn, Mn, Mg, and Fe. Iron was selected since it is involved in the electron transport process, Mg is the principal component of the chlorophyll molecule, and Mn is a vital component of the oxygen-evolving complex (OEC) of PSII.

2.4. Chlorophyll Concentration

Frozen leaf material was ground and extracted with an ice-cold 80% (*v*/*v*) acetone. After centrifugation at 5000× *g* for 10 min at 0–4 °C, the supernatant was measured spectrophotometrically (Specord 210 Plus, Ed. 2010, Analytik Jena AG, Jena, Germany). Total chlorophyll content (mg g^{-1} FW) was calculated according to Lichtenthaler [79].

2.5. Chlorophyll Fluorescence Imaging Analysis

Pulse amplitude modulation (PAM) chlorophyll fluorescence measurements were performed using the Imaging-PAM Fluorometer M-Series MINI-Version (Heinz Walz GmbH, Effeltrich, Germany). All measurements were conducted in dark-adapted (20 min) leaves of clary sage plants that were grown with 5 µM Zn (control), or with 900 µM Zn treated plants, as was previously described in detail [80]. The actinic light (AL) intensity of 900 µmol photons m^{-2} s^{-1} (4.5 times higher than the growth light intensity) was used for measuring the photosynthetic efficiency. By using Win V2.41a software (Heinz Walz GmbH, Effeltrich, Germany), the parameters explained in detail in Supplementary Table S1 were estimated. Typical color-coded images showing the whole *S. sclarea* leaf PSII responses to high light (HL) and excess Zn treatment are also presented.

2.6. Statistics

Before conducting statistical analyses, the dataset underwent normality and variance homogeneity testing using the Shapiro–Wilk and Levene tests, respectively [81]. The results indicated that the data followed a normal distribution, yet the criterion for variance homogeneity was not fulfilled. Consequently, Welch's one-way ANOVA was employed to assess the effects of Zn treatment, complemented by a Games–Howell test for post hoc examination. These statistical procedures were executed in IBM SPSS version 28.0 for Windows [82], with a significance threshold set at $p < 0.05$ for determining statistically meaningful differences.

3. Results

3.1. Elemental Content of Salvia sclarea after Zn Exposure

An increased Zn leaf content was noticed in clary sage plants exposed to 900 µM Zn (Figure 1a), in contrast to a decreased Mg leaf (Figure 1b). Leaf Zn increased by 66% after 5 days of exposure to Zn (Figure 1a), whereas at the same time, a 4% decrease in Mg leaf (Figure 1b) was noticed.

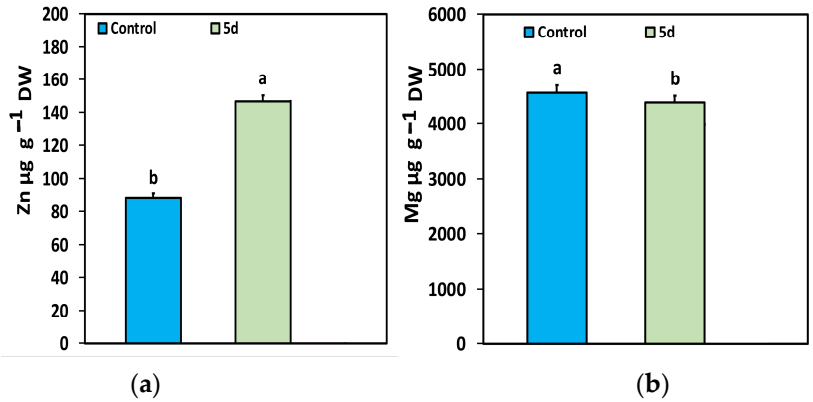

Figure 1. Changes in leaf elemental content of clary sage plants: (**a**) zinc (µg g^{-1} DW); (**b**) magnesium (µg g^{-1} DW); of control plants and after 5 days of exposure to Zn. Different letters indicate statistical differences ($p < 0.05$). Error bars symbolize SD.

Leaf Fe content in clary sage plants (Figure 2a) showed a 19% increase after 5 days of exposure to Zn, whereas Mn content at the same time increased by 95% after exposure to Zn (Figure 2b).

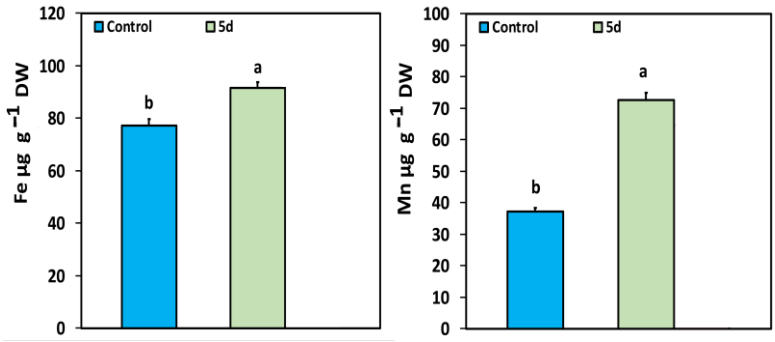

Figure 2. Changes in leaf elemental content of clary sage plants: (**a**) iron (µg g^{-1} DW); (**b**) manganese (µg g^{-1} DW); of control plants, and after 5 days of exposure to Zn. Different letters indicate statistical differences ($p < 0.05$). Error bars symbolize SD.

3.2. Impact of Zn Exposure on Chlorophyll Content, Maximum Efficiency of PSII Photochemistry and Oxygen-Evolving Complex

There were no significant changes in the chlorophyll content of clary sage plants after 3 and 5 days of exposure to 900 µM Zn, but after 8 days of exposure, chlorophyll decreased by 6% ($p < 0.05$) (Figure 3a). The functionality of the oxygen-evolving complex (OEC, F*v*/F*o*) increased after 5 days of exposure to Zn (Figure 3b), but further exposure (8 days), showed a decreased efficiency compared to 5 days, resembling the efficiency of control plants (Figure 3b). However, the OEC (F*v*/F*o*) was better functioning compared to 3 days of exposure to Zn (Figure 3b).

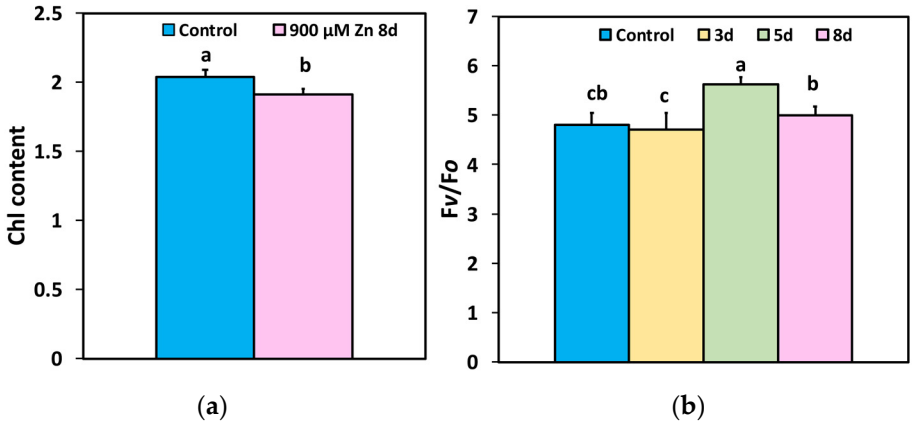

Figure 3. Effects of excess Zn on clary sage plants: (**a**) chlorophyll content of control plants and after 8 days of exposure to 900 µM Zn; (**b**) the functionality of the oxygen-evolving complex (F*v*/F*o*); of control plants, and after 3, 5, and 8 days of exposure to Zn. Different letters indicate statistical differences ($p < 0.05$). Error bars symbolize SD.

The maximum efficiency of PSII photochemistry (F*v*/F*m*) showed a comparable response pattern to that of the OEC, with increased efficiency at 5 days of Zn exposure, and at 8 days, a resemblance to the maximum efficiency of control plants (Figure 4a). This similarity of the response patterns of F*v*/F*m* and F*v*/F*o* was documented by a regression analysis that showed a positive significant correlation ($R^2 = 0.9937$, $p < 0.001$) (Figure 4b).

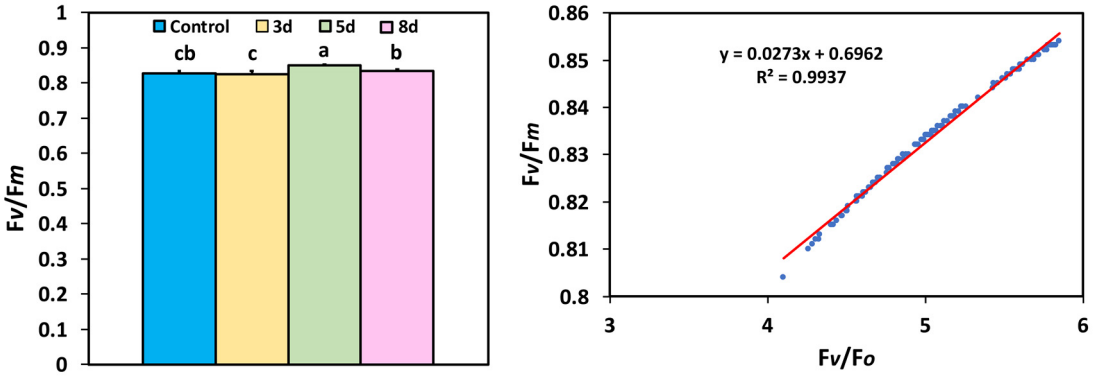

Figure 4. Effects of excess Zn on clary sage plants: (**a**) the maximum efficiency of PSII photochemistry (F*v*/F*m*) of control plants, and after 3, 5, and 8 days of exposure to Zn. Different letters indicate statistical differences ($p < 0.05$). Error bars symbolize SD. (**b**) correlation analysis between F*v*/F*m* and F*v*/F*o* of control plants, and after 3, 5, and 8 days of exposure to Zn (based on data of Figures 3b and 4a). Each blue dot represents a paired observation of the variables and the red line is a regression line that shows the trend/relationship between the two variables. The pattern of the dots and their proximity to the red line indicates a strong positive correlation.

3.3. Impact of Zn Exposure on Non-Photochemical Quenching and Light Energy Use

The absorbed light energy at photosystem II (PSII) is partitioned to Φ_{PSII}, Φ_{NPQ}, and Φ_{NO} with a sum equal to 1 [83].

The quantum yield of PSII photochemistry (Φ_{PSII}) increased by the increased duration to Zn exposure and showed a 24% rise after 8 days of exposure, as compared to control plants (Figure 5a). In contrast, the quantum yields of regulated non-photochemical energy loss in PSII (Φ_{NPQ}) decreased with increased exposure time to Zn, showing a 25% reduction after 8 days of Zn exposure (Figure 5b) compared to control plants.

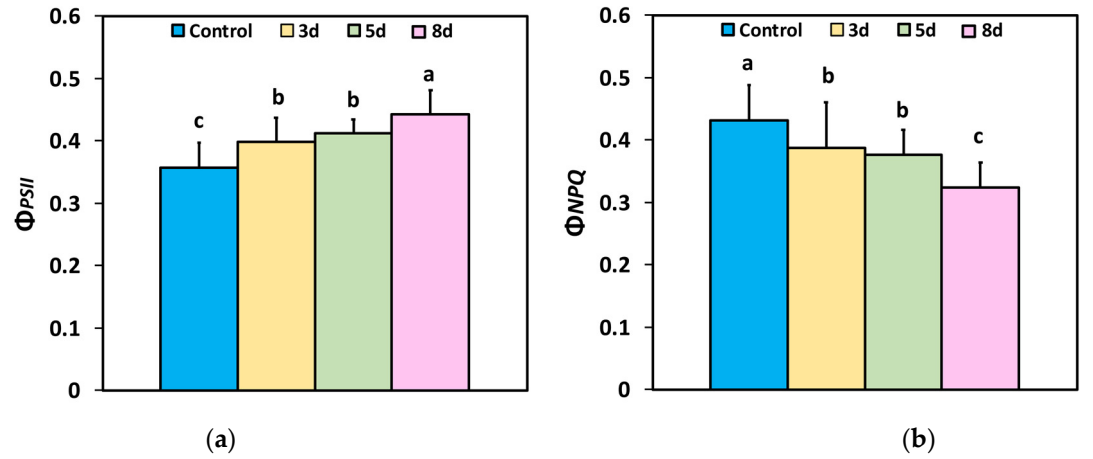

Figure 5. Changes in light energy use in clary sage plants after exposure to 900 µM Zn: (**a**) the quantum yield of PSII photochemistry (Φ_{PSII}); (**b**) the quantum yield of regulated non-photochemical energy loss in PSII (Φ_{NPQ}); of control plants, and after 3, 5, and 8 days of exposure to Zn. Different letters indicate statistical differences ($p < 0.05$). Error bars symbolize SD.

The quantum yield of non-regulated energy loss in PSII (Φ_{NO}) remained constant after 3 and 5 days of exposure to Zn, but after 8 days of exposure, showed a 10% increase ($p < 0.05$) compared to control plants (Figure 6a).

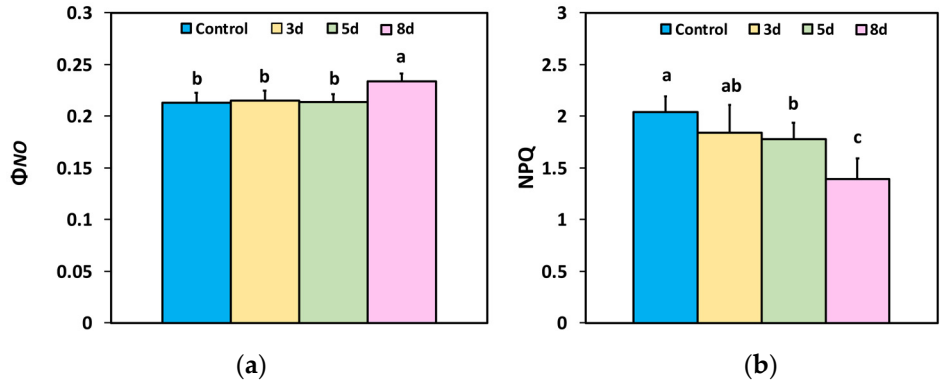

Figure 6. Changes in the quantum yield of non-regulated energy loss in PSII (Φ_{NO}) and the non-photochemical quenching (NPQ) after exposure to 900 µM Zn: (**a**) the non-regulated energy loss in PSII (Φ_{NO}); (**b**) the non-photochemical quenching (NPQ); of control plants, and after 3, 5, and 8 days of exposure to Zn. Different letters indicate statistical differences ($p < 0.05$). Error bars symbolize SD.

A time-dependent decrease in non-photochemical quenching (NPQ) was observed after Zn exposure (Figure 6b). After 8 days of exposure to Zn, NPQ was 32% lower compared to control plants.

3.4. Impact of Zn Exposure on PSII Reaction Centers and their Efficiency

The percentage of open PSII reaction centers (RC); that is, the photochemical quenching (q*p*) increased after exposure to Zn, showing a 13% higher value after 8 days of exposure to Zn (Figure 7a) as compared to the control plants. The efficiency of open PSII reaction centers (F*v*′/F*m*′) remained the same for the control plants after 3 days of exposure to Zn, but after 5 and 8 days of exposure, it increased significantly, compared to control plants (Figure 7b). After 8 days of exposure to Zn, F*v*′/F*m*′ increased by 10% compared to the control plants (Figure 7b).

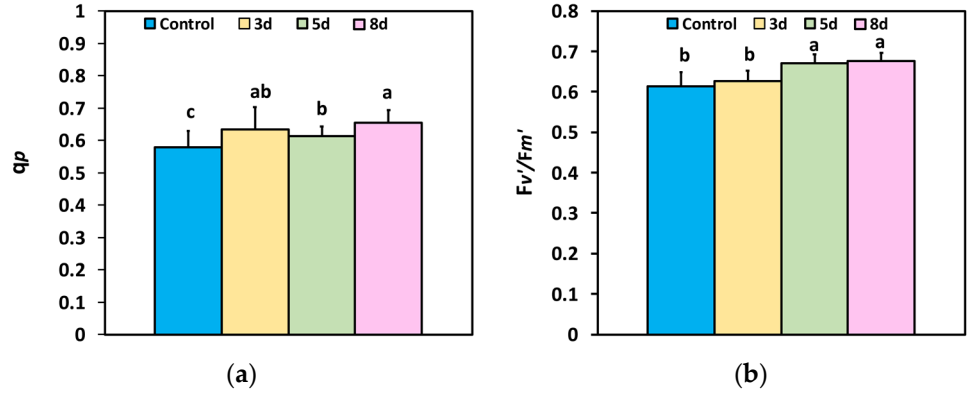

Figure 7. The percentage of open PSII reaction centers and their efficiency after Zn exposure: (**a**) the fraction of open PSII reaction centers (q*p*); (**b**) the efficiency of open PSII reaction centers (F*v*′/F*m*′); of control plants, and after 3, 5, and 8 days of exposure to Zn. Different letters indicate statistical differences ($p < 0.05$). Error bars symbolize SD.

3.5. Impact of Zn Exposure on the Excess Excitation Energy and the Electron Transport Rate

The electron transport rate (ETR) increased by prolonged exposure to Zn, showing a 24% increase after 8 days of exposure, as compared to control plants (Figure 8a). In contrast, the excess excitation energy (EXC), decreased with extended exposure to Zn, showed an 18% reduction (Figure 8b) after 8 days of exposure to Zn compared to control plants.

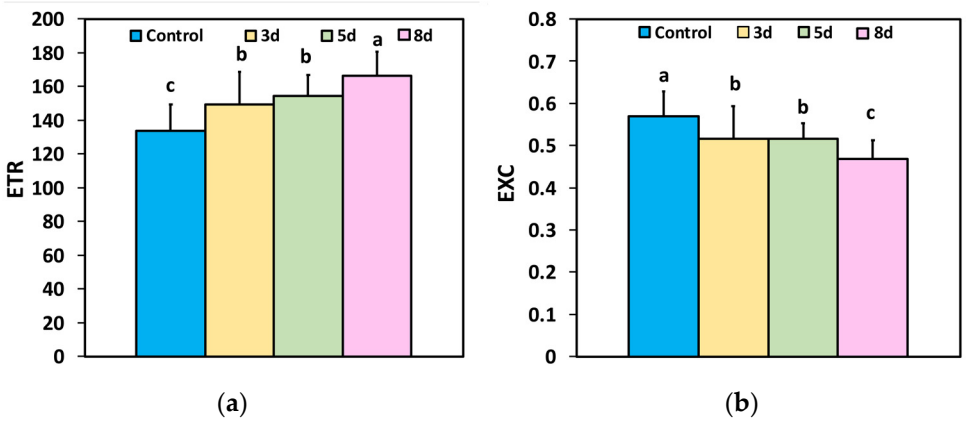

Figure 8. Changes on the electron transport rate (ETR) (**a**), and the excess excitation energy (EXC) (**b**); of control plants, and after 3, 5, and 8 days of exposure to 900 μM Zn. Different letters indicate statistical differences ($p < 0.05$). Error bars symbolize SD.

3.6. Impact of Zn Exposure on Spatial Heterogeneity of PSII Photochemistry

Exposure of clary sage plants to Zn and 900 μmol photons m^{-2} s^{-1} increased the spatial leaf heterogeneity observed mainly in the yield of photochemical energy conversion (Φ_{PSII}), showing increased mean leaf area values (Figure 9) in the yield of regulated non-photochemical energy loss (Φ_{NPQ}), displaying decreased mean leaf area values (Figure 9), and in the fraction of open PSII reaction centers (q*p*), presenting an increased portion of open RC. The spatiotemporal heterogeneity that was observed was more pronounced after 8 days of exposure to Zn, with leaf edges possessing the higher q_P values, i.e., the higher fraction of open PSII RC (Figure 9). The area on leaf edges with the higher values of q_P was accompanied by higher values of Φ_{PSII} and lower values of Φ_{NPQ}. In contrast, the adjacent cells of major veins with lower values of q_P were accompanied by lower values of Φ_{PSII} and higher values of Φ_{NPQ} (Figure 9).

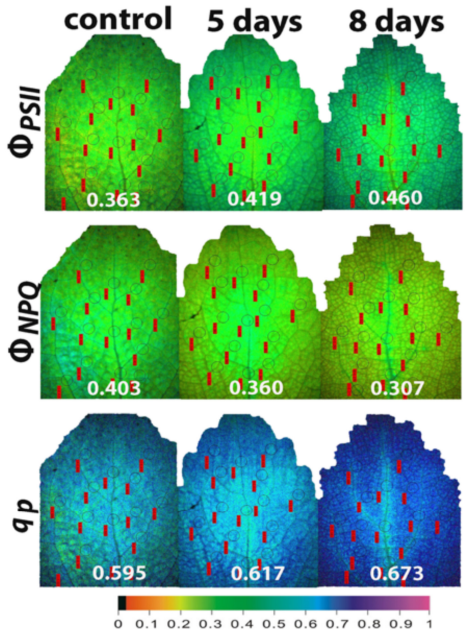

Figure 9. Representative color-coded leaf images of PSII functionality after exposure of clary sage plants to Zn and 900 μmol photons m^{-2} s^{-1}. Φ_{PSII}, $\Phi_{NPQ,}$ and q*p* of control plants, and after 5 and 8 days of exposure to Zn. The red labels on the leaf surface are the corresponding values of the measured chlorophyll fluorescence parameter documenting the spatiotemporal heterogeneity. A color code, representing each chlorophyll fluorescence parameter value, is shown.

4. Discussion

Excessive Zn supply in plants may impair plant growth, disturb chlorophyll synthesis, and induce nutrient imbalances [14,84]. Excess Zn supply (>300 μM) has been reported to reduce chlorophyll [3,14,29,84,85] and either sustain photosynthetic efficiency [84], enhance photosynthetic function [3,14], or restrict it [29]. The reduced chlorophyll in *S. sclarea* plants that was observed after exposure to 900 μM Zn for 8 days (Figure 3a) could be attributed to Mg decline (Figure 1b). Magnesium constitutes the primary component of the chlorophyll molecule's tetrapyrrole ring [3,86]. Chlorophyll molecules are the primary pigments responsible for light absorption and energy transfer to RC for charge separation and subsequent electron transport [35,87,88]. Mutants with diminished chlorophyll content possess smaller light-harvesting chlorophyll antennae, resulting in more efficient light partitioning and potential enhancement of photosynthetic efficiency [89]. Plants with lower chlorophyll content retain diminished antenna size, demonstrating lower NPQ [89]. Reducing chlorophyll content has been suggested as a potential mode to diminish excess light absorption and increase the efficiency of photosynthesis [82,89–93]. Enhanced efficiency of photosynthesis is accomplished via an improved distribution of absorbed light energy that also decreases oxidative stress [94]. The lower amount of energy dissipation as heat (NPQ) after 5 and 8 days of exposure to Zn (Figure 6b) is indicative of the photoprotective effect provided by the smaller light-harvesting antennae due to the reduced chlorophyll (Figure 3a). Photoprotection by NPQ is important for proper growth and plant expansion [42,82,95].

The higher efficiency of the OEC (Fv/Fo) after 5 days of exposure to Zn (Figure 3b) appeared at the same time as an increased Mn (Figure 2b). Manganese plays a crucial role in the OEC of PSII, serving in water oxidation and electron generation on the PSII donor side [3,96,97]. The higher efficiency of the OEC (Figure 3b) after 5 days of exposure to Zn corresponded to the maximum efficiency of PSII photochemistry (Fv/Fm) (Figure 4a). A decreased efficiency of the OEC leads to a decline in Fv/Fm [98,99], which was in accordance with the positive significant correlation in our regression analysis (Figure 4b).

Iron increased from exposure to Zn (Figure 2a) in a similar pattern to the increased Zn accumulation (Figure 1a), supporting the conclusion that situations stimulating the accumulation of Zn may also enhance Fe accumulation in plants [25,100]. Iron plays a vital role in the enzymes engaged in ETR [101,102]. Exposure of *S. sclarea* plants to Zn significantly increased leaf Fe levels (Figure 2a), accompanied by a rise in the ETR (Figure 8a). This increased ETR after 8 days of exposure to Zn (Figure 8a) was due to the decreased NPQ (Figure 6b) [103–105]. However, NPQ inhibits ROS formation, acting as a photoprotective mechanism [34,42,46,106–108]. The increased Φ_{NO} after 8 days of exposure to Zn (Figure 6a) implies an increased ROS production, since Φ_{NO} is regarded to be relevant to the amount of $^1O_2$ generation [3,109–111]. Singlet oxygen ($^1O_2$) is produced from triplet chlorophylls ^{3}Chl* that react with molecular oxygen [34–37]. Thus, it can be suggested that NPQ can regulate in a way the ROS level [53,56,112,113].

The increased ROS level after 8 days of exposure to Zn, as manifested by the increased Φ_{NO} (Figure 6a), suggests that it activated the molecular mechanisms that are considered beneficial for improving photosynthetic function [53,77]. ROS signaling can be positive and fundamental for plant acclimation to a change in homeostasis, controlling different pathways [114,115]. Nevertheless, the elevated levels of ROS are recognized as being detrimental to plants [34,57,116–119].

The increased Φ_{PSII} after 8 days of exposure to Zn (Figure 5a) can be attributed to both an increased fraction of open PSII RC (qp) (Figure 7a), and to an increased efficiency of these RC (Fv'/Fm') (Figure 7b) [120]. A lower fraction of open PSII RC, as observed in control plants (Figure 7a), pairs with a more reduced quinone A (Q_A) pool, corresponding to an increased stomatal opening [121,122]. The oxidation state of Q_A reflects the balance between excitation energy at PSII and the rate of the Calvin–Benson–Bassham cycle [122].

The reduced EXC at PSII after 8 days of exposure to Zn (Figure 8b) was due to the increased Φ_{PSII} (Figure 5a) and ETR (Figure 8a), demonstrating enhanced PSII efficiency.

Boosting the photosynthesis of crop plants to meet the immense global food demand poses a significant challenge for plant scientists [123–125]. Therefore, enhancing the photosynthetic efficiency of crop plants stands as a pivotal and highly significant research endeavor [90,92]. The objective of improving photosynthetic efficiency can be realized through the improved distribution of absorbed light energy [126].

Zinc (Figure 1a) and Fe (Figure 2a) accumulation in the leaves of *S. sclarea* increased after exposure to Zn, but leaf Mg decreased (Figure 1b). There are a lot of data published about the interplay of Zn with other elements [2,3,14,27,100,127–130]. Plants serve as the primary source of Zn in the human diet, and human Zn deficiency contributes to over 400,000 deaths annually [8]. Excess Zn application can be utilized as a tool to enhance plant growth and crop yields and increase plant biomass production, providing food and energy safety for a population that is constantly increasing [3].

Micronutrient deficiencies, notably of Zn and Fe, persist as critical public health challenges affecting over 3 billion people globally [131]. The deficiency in these elements is often due to the nutrient-poor status of agricultural soils, posing a severe threat to nutritional adequacy [131]. Zinc deficiency, in particular, poses a significant risk to approximately 1/3 of the worldwide population, with countries like Turkey, China, Pakistan, and India facing severe Zn deficiency symptoms [132].

Exposing *S. sclarea* plants to 900 μM Zn established not only an increased Zn but also an elevated iron content in the leaf tissues. Increased Fe may act to alleviate toxicity effects on photosynthetic ETR [133]. Zinc and Fe are crucial micronutrients essential for human health [134]. Consequently, subjecting crops to excess Zn in hydroponics could be deemed an economical approach to addressing these nutritional deficiencies [134].

Plants have several mechanisms that permit effective acclimation to HL intensities [135,136]. Although HL can enhance photosynthesis, it can also produce injury or inactivation of photosynthetic procedures (photoinhibition), especially in combination with other stresses [137]. Previous observations have highlighted that foliar Zn application enhances photoprotective mechanisms in drought-stressed wheat plants [138], whereas excess Zn (900 μM) application in *S. sclarea* under LL enhanced NPQ values [3], documenting Zn's suitability for enhancing photoprotection [139]. However, under HL, excess Zn (900 μM) application decreased NPQ values (Figure 6b), providing evidence of the photoprotection offered by the smaller light-harvesting antennae due to the reduced chlorophyll (Figure 3a). Thus, the excess Zn application offers a better choice for enhanced PSII photochemistry under HL than under LL. It is well known that HL-grown plants have smaller light-harvesting antennae than LL-grown plants for photoprotection [140,141]. It seems that the smaller light-harvesting antennae offer more advantages to plants grown at HL than at LL. When chlorophyll content is limited, only RC accumulate chlorophyll to retain their function [140].

Enhancing photosynthesis is widely accepted as critical to advancing agricultural productivity [90,123,124]. Efforts to boost photosynthetic efficiency are intended to enhance light energy utilization by redesigning the mechanisms to dissipate excess excitation energy [142]. The decreased NPQ after 5 and 8 days of exposure to Zn (Figure 6b) resulted in an increased ETR (Figure 8a). The enhancement of ETR by 24%, after 8 days of exposure to Zn (Figure 8a), will possibly result in a substantial impact on plant biomass production. For example, an enhancement of ETR by 20% resulted in an increase in the yield of sorghum by 8% [142] and the yield of wheat by 7.3% [143].

Excess Zn altered photosynthetic function and increased ROS production in *Handroanthus impetiginosus* and *Tabebuia roseoalba* [144]. The decline of *Carthamus tinctorius* growth under excess Zn was correlated to decreased photosynthetic function and antioxidant response to oxidative stress [31]. The response of plants to excess Zn depends on the tolerance or sensitivity of the species to heavy metal toxicity [145]. Common bermudagrass (*Cynodon dactylon*) [146], white mustard (*Sinapis alba*) [147], and clary sage (*Salvia sclarea*) [14], have been characterized as Zn-tolerant species with implications for phytoremediation of Zn-contaminated soils. Clary sage is a heliophilous herbaceous plant species [148], showing

high adaptability in the Mediterranean area [74], and being of great interest to the aromatic and medicinal industries [149]. In addition, it is an economically noteworthy plant species for phytostabilization and phytoextraction of Zn-contaminated soils [14].

Under LL intensity and high Zn exposure, the production of ROS in clary sage plants, evaluated by chlorophyll fluorescence imaging, was reduced, comparable to optimum Zn supply [3]. However, in this experiment, the same Zn concentration under HL intensity resulted in increased ROS production, as observed by the increased Φ_{NO} (Figure 6a). It is suggested that the increased $^1O_2$ production (Figure 6a) initiated antioxidant response signaling for redox regulation [150]. This increased $^1O_2$ production is considered beneficial for enhancing photosynthetic function through enhancing the repair of photodamaged PSII [151]. Singlet oxygen signaling has been recognized to control plant responses to HL stress and control oxidative stress [152]. ROS are considered to play crucial roles as signaling molecules in the initiation of stress-response networks, thus contributing to the establishment of protection mechanisms and plant acclimation and resilience [34,57,114,115,153].

5. Conclusions

After 8 days of exposure of *S. sclarea* plants to Zn, the increased Φ_{PSII} (Figure 5a) and ETR (Figure 8a), under HL intensity, resulted in reduced EXC at PSII (Figure 8b), demonstrating an enhancement of PSII efficiency. The increased Φ_{PSII} (Figure 5a) was attributed to both an increased fraction of open PSII RC (q*p*) (Figure 7a), and to an increased efficiency of these RC (F*v*′/F*m*′) (Figure 7b). It is suggested that the decreased NPQ induced acclimation responses of clary sage plants to HL and excess Zn by increasing $^1O_2$ production.

The findings from this research offer approaches to enhance both Fe and Zn accumulation in aromatic and medicinal plants while improving their photosynthetic capabilities. Excess Zn application, predominantly under HL, can be utilized as a tool to improve plant growth and crop yields and increase plant biomass production, providing food and energy safety.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy14030589/s1, Table S1: definitions of the chlorophyll fluorescence parameters used in the experiments.

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