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Research Article /Araştırma Makalesi

Dissection of the photosynthetic efficiency by JIP test in sunflower plants under heat stress

Isı stresi altındaki ayçiçeği bitkilerinde fotosentetik verimliliğin JIP testi ile incelenmesi

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Abstract

In this study, the photochemical responses of sunflower (*Helianthus annuus* L. cv. Aitana) plants under moderate and severe high temperature stress (45°C and 55°C, 4 hours) at the early seedling stage were investigated using the chlorophyll a fluorescence technique and the JIP test. The results showed severe heat stress had a more pronounced inhibitory effect on photosynthetic electron transport reactions in sunflower cotyledons than moderate heat stress. The increase in Fo parameter and the decrease in *Fm, Fv/Fo, Fv/Fm, φo, and φo/(1-φo)* parameters caused by severe heat stress revealed that primary photochemical reactions in sunflower cotyledons were significantly inhibited. In addition, the increase observed in the ΔV/Δto and TRo/RC parameters indicated that severe heat stress significantly inhibited the oxidation ability of the reaction centers in photosystem II units but elevated the amount of the trapped light energy in sunflower cotyledons. Increased *φDo and DIo*/RC parameters in sunflower cotyledons under severe heat stress prove that the trapped light energy cannot be used in electron transport reactions and is dissipated as heat. Severe heat stress resulted in insufficient reduction of the plastoquinone pool in sunflower cotyledons, as indicated by the decrease in the parameter area. As a result, it could be concluded that severe heat stress almost completely inhibits photosynthetic activity in sunflower cotyledons by adversely affecting light absorption, the transport of absorbed light energy to the reaction centers of photosystem II units, and the delivery of electrons to photosystem I units.

Keywords: Chlorophyll a fluorescence; heat stress; *Helianthus annuus*; JIP test; sunflower

Öz

Bu çalışmada, ayçiçeği (*Helianthus annuus* L. cv. Aitana) bitkisinin erken fide evresinde orta dereceli ve şiddetli yüksek sıcaklık stresi (45°C ve 55°C, 4 saat) altındaki fotokimyasal cevapları klorofil a floresansı tekniği ve JIP testi kullanılarak araştırılmıştır. Sonuçlar, ayçiçeği kotiledonlarındaki fotosentetik aktiviteyi orta dereceli yüksek sıcaklık stresi ile karşılaştırıldığında şiddetli yüksek sıcaklık uygulamasının daha olumsuz yönde etkilediğini göstermiştir. Şiddetli yüksek sıcaklık stresi ayçiçeği kotiledonlarındaki Fo değerinin artmasına; *Fm, Fv/Fo ve Fv/Fm* değerlerinin ise azalmasına neden olmuştur. Bu değişimler ayçiçeği bitkilerindeki elektron taşınım reaksiyonlarının önemli derecede fotoinhibisyona uğradığını göstermektedir. Şiddetli yüksek sıcaklık stresi ayrıca ayçiçeği kotiledonlarında, φV/φto ve TRo/RC parametrelerindeki artışlarla da gösterildiği gibi,

fotosistem II birimlerindeki reaksiyon merkezlerinin oksidasyon yeteneğini inhibe ettiğini ve yakalanan ışık enerjisi miktarını artırdığını götermiştir. Şiddetli yüksek sıcaklık stresine maruz bırakılan ayçiçeği kotiledonlarındaki *DIo/RC* ve Δ*Do* değerlerinin artması, yakalanan enerjinin fotokimyasal olaylarda kullanılmadığını ve ısı olarak kaybedildiğini göstermektedir. Buna bağlı olarak alan parametresindeki azalma, plastokinon havuzunun yeterince indirgenemediğini ortaya çıkarmıştır. Sonuç olarak, şiddetli yüksek sıcaklık stresinin ayçiçeği bitkilerinin kotiledonlarındaki fotosistem II aktivitesini ve ışık absorbsiyonunu olumsuz yönde etkileyerek, absorblanan ışık enerjisinin fotosistem II reaksiyon merkezlerine taşınımını ve elektronların fotosistem I birimlerine iletilmesini inhibe ederek ve fotosentetik verimi azalttığı sonucuna varılabilir.
Anahtar Kelimeler: Klorofil a floresansı; ısı stresi; *Helianthus annuus;* JIP testi; ayçiçeği

Introduction

Rising temperatures due to climate change have seriously threatened agricultural productivity worldwide, as well as the geographical distribution of plant species. Radiative forcing, responsible for the increase in the amount of energy in the atmosphere due to the accumulation of greenhouse gases, is the leading cause of global warming (Jagadish et al., 2021). Over the last 250 years, the accumulation of CO2 and methane gas in the atmosphere has increased by approximately 30% and 150%, respectively (Friedlingstein et al., 2010), which is likely to result in increased global temperatures (Sehgal et al., 2016). Thus, it is inevitable that the increase in temperature on Earth will affect the phenology, physiological efficiency, and productivity of plants. In addition, it has been predicted that severe heat waves will more frequently occur due to climate change, thereby causing decreases in the growth, yield, and survival of crop plants (Ortiz-Bobea et al., 2019). On the other hand, as the world population hits approximately 9 billion in 2050, the global food demand has been estimated to increase by 100-110% (Haider et al., 2020). The restrictive effect of global warming on agricultural productivity also increases the likelihood that the world's population will face the risk of malnutrition, which urgently requires investigating the responses of plants to heat stress multifacetedly.

In studies on “heat stress”, or “heat shock”, plants have been exposed to temperatures approximately 20°C higher than the optimum temperature for a short period (hours or shorter), aiming at the emergence and observation of rapid responses to heat stress in plants (Mittler et al., 2012). Such studies, which are not very realistic in an ecological sense, are essential in gaining insight into the mechanisms related to plants' perception and tolerance of heat stress. Regardless of the mode of application, plants are affected by high-temperature conditions due to their sessile lifestyle and poikilotherm characteristics. It has been well elucidated that heat stress adversely affects root and shoot growth, biomass accumulation, cellular structures, phytohormone profile, membrane integrity, respiration, photosynthesis, photosynthetic pigments, gene expression, osmolyte content, and primary and secondary metabolites in several plant species, which consequently causes a decreased plant productivity (Allakhverdiev et al., 2008; Binder & Patterson, 2009; Ruan et al., 2010; Sharkey & Zhang, 2010; Doğru, 2021). Such changes sometimes cause the disruption of cellular organization and even cell death in plants under heat stress, whereas it is sometimes regarded as plastic metabolic responses, which ensures that the plant acquires heat tolerance.

Temperature increases must be perceived by distinct signaling pathways and then transduced into physiological responses in plants (Kan et al., 2023). However, the way of this mechanism is still unclear. It has been reported that the amounts of active oxygen species (AOS), ethylene, phytohormones, and Ca^{2+}, as well as the changes in protein conformation and DNA and RNA sequence, could be putative thermosensors in plants under heat stress. (Kan et al., 2023). Recently, the “membrane sensor hypothesis” has been put forward due to the observation that changes in the structural properties of the plasma membrane may induce heat stress responses without heat shock proteins-induced

protein denaturation in plants (Li et al., 2018). Therefore, the sustained function of biological membranes is essential for plants under heat stress conditions to maintain several metabolic processes, including photosynthesis.

It has been well known that severe heat stress inhibits redox reactions by causing structural disruptions in thylakoid membranes in chloroplasts (Biswal et al., 2011). Therefore, the thylakoid membrane system could host some microdomains sensing the changes in membrane fluidity in the lamellae under heat stress, which would probably earn them the title of the "photosynthetic thermometer." Wise et al. (2004) have demonstrated that the primary target of heat stress injury is the photosynthetic electron transport reactions in the thylakoid lamellae and carbon metabolism in the stroma of chloroplasts. It has been declared that heat stress significantly inhibited photosystem II (PSII) activity due to physical changes in thylakoid membranes, which host PSII units (Camejo et al., 2005). Such effects of heat stress on photosynthetic apparatus might be associated with the accelerated rate of AOS accumulation (Xiaochuang et al., 2017). AOS are highly reactive compounds and could damage some proteins and lipids located in the thylakoid membranes and involved in electron transport reactions. Thus, there is an interesting feedback loop between AOS accumulation and photosynthetic electron transport under heat stress conditions, which amplifies each other. These data suggested that heat stress reduces photosynthetic activity directly and indirectly in plants. Therefore, examining the changes in photosynthetic activity in plants under stress is essential. Today, chlorophyll a fluorescence and the JIP test have been reported to be the most modern and reliable techniques for measuring photosynthetic efficiency, particularly PSII activity (Doğru & Çakırlar, 2020). Details regarding the application of the JIP test are stated elsewhere (Kalaji et al., 2011; Doğru, 2021).

Sunflower (*Helianthus annuus* L.), a member of the family Asteraceae, is an annual oilseed crop grown on 24.77 million hectares worldwide with an average yield of 44.31 million metric tonnes and contributes to approximately 8% of the world oilseed production (Ameen et al., 2024). Sunflower oil is ideal for the human diet because it contains higher levels of polyunsaturated fatty acids, vitamin E, and polyphenols (Catiempo et al., 2020). Sunflower, the fourth most important oil crop worldwide, is adaptable to moisture, soil type and composition, and agricultural practices (Ameen et al., 2024). However, it has been stated that sunflower is sensitive to heat and drought stresses during its growing cycle, thereby severely reducing yield (Debaeke et al., 2017).

Accordingly, this study aims to examine the photochemical changes caused by moderate and severe heat stress in sunflower plants using the chlorophyll a fluorescence technique and the JIP test. In addition, we demonstrated which steps of the photosynthetic electron transport reactions are affected by heat stress, thereby providing a mechanistic framework.

Material and methods

Plant material, growth conditions and experimental design

In this study, a sunflower (*Helianthus annuus* L.) hybrid variety, Aitana, was used. This variety is an oilseed and linoleic type that can be used for rotation purposes. Depending on ecological conditions, cultivation techniques, soil structure, and irrigation amount, its average height is 128-174 cm, table diameter is 21-31 cm, thousand-grain weight is 40-78 g, seed yield is 300-528 g da-1, oil content is 44-44.5%, and oil yield is 131-234 kg da-1 (Yılmaz & Kınay, 2015; Deviren & Eryiğit, 2017). The seeds were obtained from the local seed suppliers and first surface-sterilized with a 5% sodium hypochlorite solution for 30 min. Then they were washed three times and imbibed in distilled water for 24 h. After imbibition, the seeds with root protrusion were sown in plastic pots containing only perlite and watered with half-strength Hoagland solution (Hoagland, 1920). Plants were grown in a growth chamber at 27/22°C day/night temperature, 16-h photoperiod, irradiance of 200 µmol m-2 s-1, -and 40-45% relative humidity. At the 10th day of growth, sunflower plants in the early seedling stage (VE) were exposed to moderate (45°C) and severe (55°C) heat stress as a heat shock for 4

hours. Chlorophyll a fluorescence measurements were taken on the intact plants 24 hours after the 4-hour heat shock treatment was completed.

Chlorophyll a fluorescence measurements

Chlorophyll a fluorescence measurements were performed with the Handy PEA fluorimeter (HandyPEA chlorophyll fluorimeter, Hansatech Instruments Ltd., Pentney, Kings Lynn, Norfolk, England). Sunflower seedlings were pre-darkened for 45-60 min at room temperature. Chlorophyll a fluorescence induction transients were measured on the cotyledons when they were exposed to a strong light pulse (3,500 µmol photons m-2 s-1). The data were analyzed and the JIP test was conducted using Biolyzer software (Strasser et al., 2000). Measurements of chlorophyll a fluorescence were done on 10 plants from each treatment, and we had 3 replicates for each plant (n=30). Identification of some chlorophyll a fluorescence and JIP test parameters are presented in Table 1.

Statistical analysis

Experiments were a randomized complete block design with three independent replicates. Analysis of variance (ANOVA) was performed using SPSS 20.0 statistical software for Windows. To separate significant differences between means, Duncan's multiple range test was used at $p < 0.05$ (Duncan, 1955).

Table 1. Identification of some chlorophyll a fluorescence and JIP test parameters

Parameters	Definition
Fo	Minimum chlorophyll a fluorescence intensity measured when all PSII reaction centers are open
Fm	Maximum chlorophyll a fluorescence intensity measured when all PSII reaction centers are closed
Fv	Varible chlorophyll a fluorescence (Fm-Fo)
Fv/Fm	Maximum quantum efficiency of PSII
Fv/Fo	A value that is proportional to the activity of the water-splitting complex on the donor side of PSII (the efficiency of Hill reaction or photolysis)
ABS/RC	Light absorbtion flux (for PSII antenna chlorophylls) per reaction center (RC)
ETo/RC	Maximum electron transport flux (further than QA-) per PSII reaction center (RC)
TRo/RC	Trapped (maximum) energy flux (leading to QA reduction) per reaction center (RC)
DIo/RC	Dissipation energy flux per PSII reaction center (RC)
RC/ABS	Density of active reaction centers per PSII antenna chlorophyll
TR/ABS	Trapped (maximum) energy flux per PSII ABS
ET/ABS	Electron transport flux per PSII ABS
DI/ABS	Dissipated energy flux per PSII ABS
RC/ABS	Density of active reaction centers per PSII antenna chlorophyll
Area	The area above the chlorophyll a fluorescence curve between Fo and Fm (reflecting the size of plastoquinone pool)
ΔV/Δto	The rate of accumulation of closed reaction centers
N	The number indicating how many times QA is reduced while fluorescence reaches its maximal value
PI_{ABS}	Performance index
SFI_{ABS}	An indicator of PSII "structure and functioning"
SM	The energy necessary for the closure of all reaction centers
$\psi 0$	The efficiency of a trapped exciton to move an electron from QA to the electron transport system

Table 1. Continued

φPo	Maximum quantum yield for primary photochemistry
φEo	Quantum yield of electron transport from QA to PQ
φDo	Quantum yield of thermal dissipation
kN	The non-photochemical de-excitation rate constant in the excited antennae for non-photochemistry
kP	The photochemical de-excitation rate constant in the excited antennae of energy fluxes for photochemistry
φo/(1-φo)	A "conformation" term for primary photochemistry
ψo/(1-ψo)	A "conformation" term for thermal reactions (non-light dependent reactions)

Results and Discussion

The results of this study indicated that the photosynthetic efficiency of the sunflower plants was negatively affected, particularly by severe heat stress, based on the changes in the chlorophyll a fluorescence and JIP test parameters. The gradually decreasing level of the Hill reaction (as shown by Fv/Fo) with increasing temperature in sunflower plants suggests that electron movement from the oxygen-evolving complex (OEC) to the PQ pool is limited by heat stress (Figure 1a), which is probably due to heat-induced structural damage in the OEC (Doğru et al., 2021). Our results are in accordance with the findings of Yamomoto (2016), who demonstrated that heat stress destabilized the four manganese-calcium clusters at the donor side of PSII, resulting in severe damage to D1 and D2 proteins and dissociation of extrinsic PsbO and Q proteins. In addition, Laloi et al. (2006) have illustrated that the accumulation of H_2O_2 and hydroxyl radicals on the donor side of PSII due to heat stress inhibits water oxidation. Similarly, the inhibitory effect of the severe heat stress on the electron flux rate to the PQ in sunflower plants is also confirmed by the diminished level of the parameter area in this study (Figure 1b), as reported earlier by Oukarroum et al. (2015). It has been well known that the maximum quantum efficiency of PSII [as indicated by Fv/Fm; Fv/Fm=(Fm-Fo)/Fm] is close to 0.83 in plants under optimum environmental conditions. In the present study, the moderate and severe heat stress considerably decreased the Fv/Fm ratio in sunflower plants (Figure 1c), indicating that a large extent of photoinhibition has occurred in PSII units (Meravi and Prajapati, 2018), which is also verified by the reduced level of maximum quantum yield of primary photochemistry (φPo) (Figure 1d). However, the intensity of the photoinhibition was more significant in the case of severe heat stress compared to moderate heat stress. Changes in the Fv/Fm ratio are proportional to changes in the parameters of Fo and Fm. It has been reported that several stress factors could be responsible for the increase in Fo (Maxwell and Johnson, 2000). Meravi & Prajapati (2018), for example, claimed that a higher level of Fo may be attributed to an increase in the fraction of PSII reaction centers that are in the inactivated state. Kalaji et al. (2011) have shown that the reason for the higher Fo values is the slowing down of the transport of electrons from QA to QB and/or the decrease in the efficiency of PSII to capture light energy. In this study, only severe heat stress led to a significantly higher Fo value in sunflower plants than in the control group (Figure 1e). Accordingly, it could be deduced that severe heat stress damaged PSII reaction centers and decreased the quantum yield of electron transport (φEo) in sunflower plants (Figure 1f), as confirmed by higher ABS/RC and lower RC/ABS values in this study (Figure 2a and b).

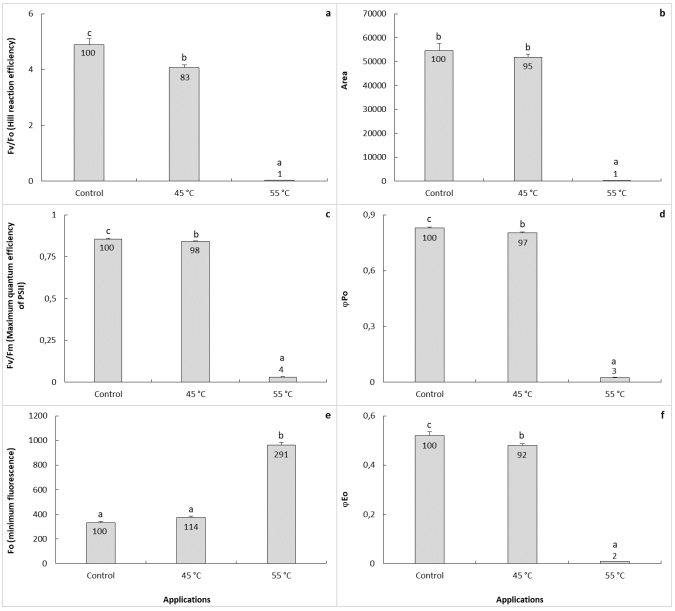

Figure 1. The effect of heat shock treatments on (a) Fv/Fo, (b) area, (c) Fv/Fm, (d) φPo (e) Fo, and (f) φEo in sunflower plants. [Columns with different letters mean significant differences between the treatments according to Duncan's multiple range test (P<0.05), and numbers inside the columns indicate % change relative to control, control = 100].

In addition, the severe heat stress increased the accumulation of the closed reaction centers in sunflower plants, as confirmed by higher *ΔV/Δto* and lower Sm values (Figure 2c and d). These results clearly indicate that intact reaction centers cannot be easily oxidized due to severe heat stress. Consequently, electron movement into QA is slowed down, and the reduction/oxidation cycle of QA is inhibited by severe heat stress, as shown by a lower level of N (Figure 2e). Under these circumstances, photosynthetic electron transport reactions further than QA are also restricted; hence, severe heat stress entirely inhibited ψo (Figure 2f).

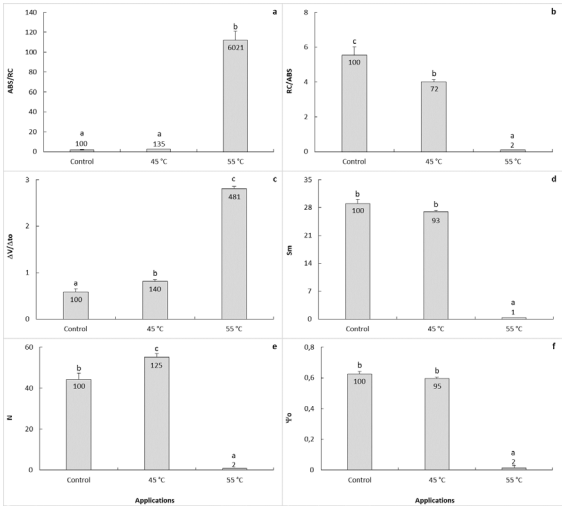

Figure 2. The effect of heat shock treatments on (a) ABS/RC, (b) RC/ABS, (c) *ΔV/Δto*, (d) Sm, (e) N, and (f) ψo in sunflower plants. [Columns with different letters mean significant differences between the treatments according to Duncan's multiple range test (P<0.05), and numbers inside the columns indicate % change relative to control, control = 100].

TRo/RC and *ETo/RC* were significantly increased by moderate heat stress compared to the relative controls in sunflower plants (Figure 3a and b), whereas *DIo/RC* was unaffected (Figure 3c). These results imply that sunflower plants under moderate heat stress more effectively trap the light energy and can photochemically quench it for electron transport reactions, as confirmed by the constant levels of *DIo/RC* (Figure 3c). However, the severe heat stress significantly elevated *TRo/RC, DIo/R*C, and φDo in sunflower plants (Figure 3a, c and d), whereas *ETo/RC* was diminished (Figure 3b), which suggests that the trapped light energy does not trigger the electron transport reactions but is non-photochemically dissipated as heat. The synchronous decrease in kP and increase in kN in sunflower plants also confirmed the existence of an inverse relation between photochemical and non-photochemical quenching under severe heat stress (Figure 3e and f).

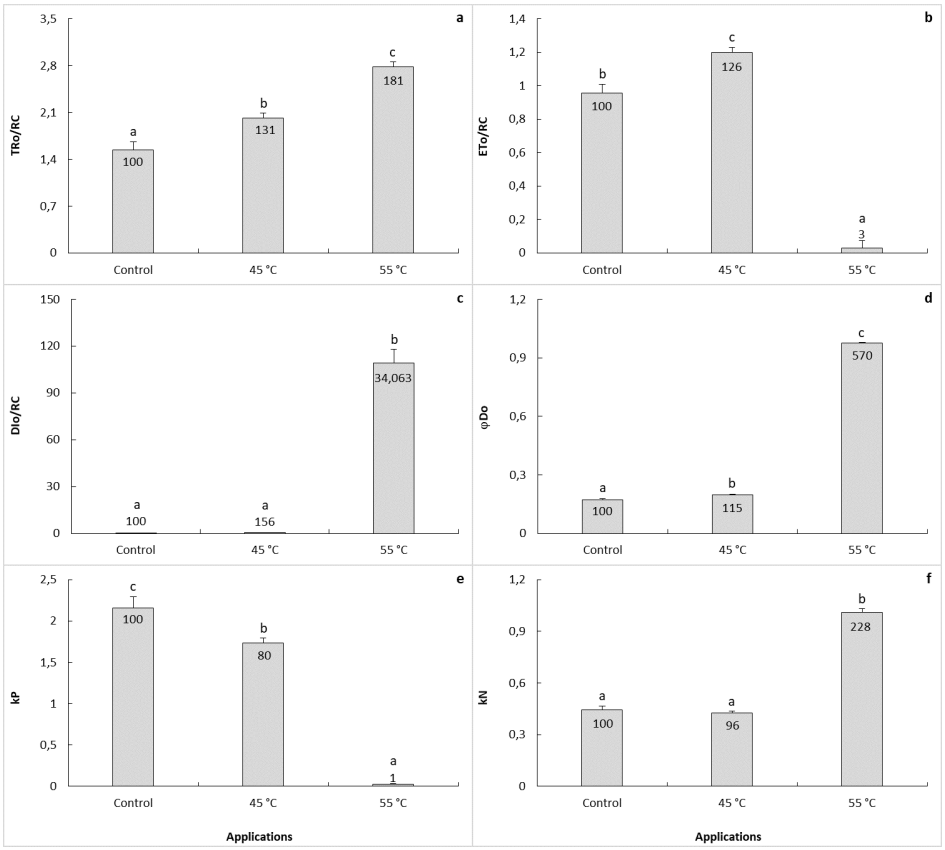

Figure 3. The effect of heat shock treatments on (a) *TRo/RC,* (b) *ETo/RC,* (c) *DIo/RC,* (d) φDo, (e) kP, and (f) kN in sunflower plants. [Columns with different letters mean significant differences between the treatments according to Duncan's multiple range test (P<0.05), and numbers inside the columns indicate % change relative to control, control = 100].

Consequently, the primary photochemical reactions and non-light-dependent reactions were severely reduced, as pointed out by the lower values of φo/(1-φo) and ψo/(1-ψo), respectively (Figure 4a and b) (Gupta, 2020). On the other hand, the moderate heat stress significantly decreased φo/(1-φo) while it did not affect ψo/(1-ψo) in sunflower plants, which may indicate a regulatory mechanism to establish an adjustment between the rates of the primary photochemistry and non-light dependent reactions. In addition, this regulative mechanism may be directly related to photochemical quenching but independent of non-photochemical quenching because

kP is considerably decreased by moderate heat stress, whereas kN is unaffected. SFIABS provides information about the structural and functional status of PSII. PIABS, on the other hand, is considered an indicator of the vitality of photosynthetic performance in plants. In this study, SFIABS and PIABS were gradually decreased as the temperature was elevated (Figure 4c and d), demonstrating that PSII units in the leaves of the maize plants were structurally damaged, leading to functional failure.

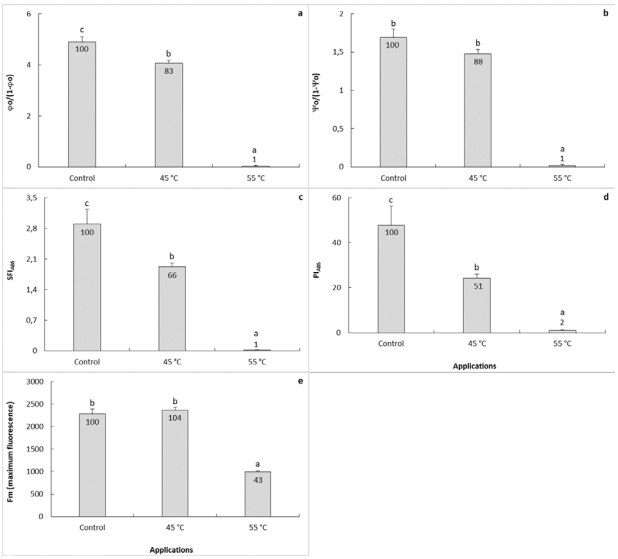

Figure 4. The effect of heat shock treatments on (a) $\varphi o/(1-\varphi o)$, (b) $\psi o/(1-\psi o)$, (c) SFIABS, (d) PIABS, and (e) Fm in sunflower plants. [Columns with different letters mean significant differences between the treatments according to Duncan's multiple range test (P<0.05), and numbers inside the columns indicate % change relative to control, control = 100].

The highest level of Fm value sunflower plants, on the other hand, suggested that the restrictive effect of severe heat stress on the photosynthetic electron transport reactions in the PSII acceptor side appeared (Figure 4e), as indicated by Georgieva & Lichtenthaler (1999) and Doğru & Çakırlar (2020). In addition, the results of this study clearly indicated that the decline in the Fv/Fm ratio in the severely heat-stressed sunflower plants was primarily due to an increase in Fo, suggesting a higher level of the accumulation of the inactive reaction center. This is also verified by the phenomenological yield model analysis, which showed that the damage in PSII reaction centers increases as the applied temperature is elevated in this investigation (Figure 5).

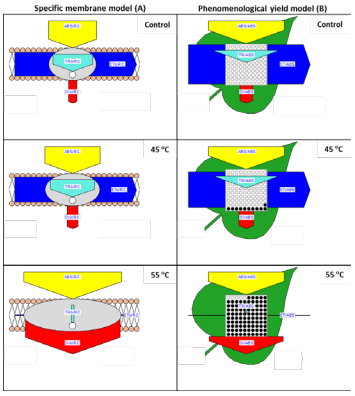

Figure 5. Presentation of some JIP test parameters by (A) specific membrane model and (B) phenomenological yield model in the sunflower plants exposed to heat shock. [In (b), empty circles indicate the intact reaction centers, while dark circles indicate the damaged reaction centers].

The JIP test allows us to analyze the OJIP chlorophyll a fluorescence transients quantitatively. It offers a better understanding of changes in the specific time points of the photosynthetic electron transport reactions. In our study, sunflower plants represented a typical polyphasic rise in terms of the chlorophyll a fluorescence transients (the OJIP curve) under control conditions. The "O-J" phase, indicating electron flux in the primary quinone acceptor QA, was morphologically similar but quantitatively different in sunflower plants under moderate heat stress from the control group (Figure 6). However, the primary photochemistry in sunflower plants under moderate heat stress was slightly but considerably diminished by the moderate heat stress, as demonstrated by the lower φPo and φo/(1-φo) in this study.

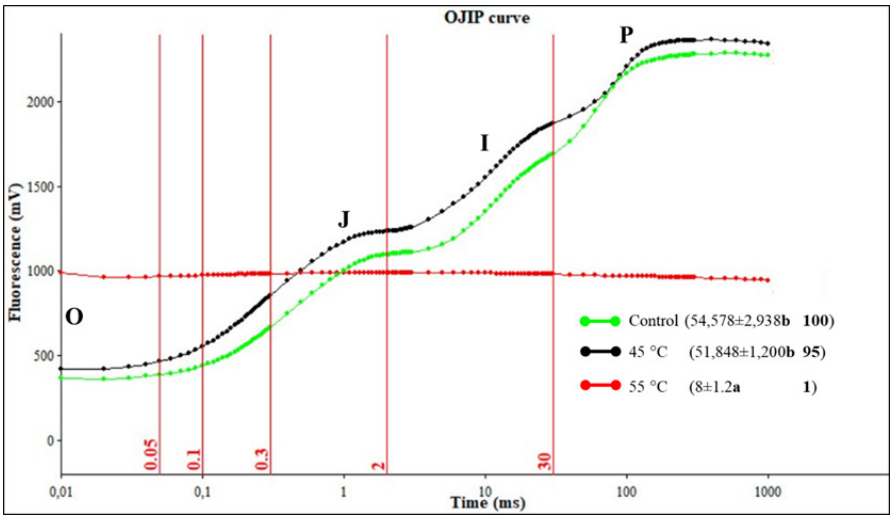

Figure 6. Chlorophyll a fluorescence induction curve of the heat-stressed sunflower plants. [Numbers in the parenthesis indicate mean values of the parameter area (area between Fo and Fm in the curve)± standart error, and different letters mean significant differences between the applications according to Duncan's multiple range test ($P<0.05$). Bold numbers at the right side indicate % change relative to control, control = 100].

A similar alteration trend in sunflower plants under moderate heat stress was also observed in the "J-I" phase, representing the characteristic efficiency of the Hill reaction, which resulted in the Fv/Fo ratio (Kumar et al., 2020). Finally, the rise between step "I" and step "P" is considered the reduction state of the ferredoxin and a measure of the PSI abundance in proportion to PSII (Lotfi et al., 2020). In our study, the observed alteration in the "I-P" step indicates the reduction of the ferredoxin is temporally different in the moderately heat-stressed sunflower plants from the control plants (Fig. 6). However, the severe heat stress enormously altered the shape of the chlorophyll a fluorescence curve in sunflower plants, demonstrating its devastating effects on entire steps of the photosynthetic light phases. Our results showed that all phases and peaks were lost due to severely heat-stressed sunflower plants, confirming that the photosynthetic electron transport was inhibited.

Conclusion

In summary, the results of this study illustrated that electron transport reactions in PSII units in cotyledons of sunflower plants were significantly inhibited due to heat stress. In general, severe heat stress had more destructive effects on photosynthetic electron transport reactions in sunflower plants in comparison with moderate heat stress. Severe heat stress led to the increased level of the accumulation of the inactive reaction centers and decreases the efficiency of PSII to capture light energy.

In addition, severe heat stress inhibited primary photochemistry and stimulated non-photochemical reactions. Consequently, the absorbed light energy could not be used to drive photochemical reactions and excess energy was quenched non-photochemically as heat. According to the changes in some JIP test parameters such as 0, Eo, ETo/RC, SFIABS and PIABS under severe heat stress, it may be concluded that photosynthetic electron transport reactions were completely inhibited by 55 ºC. Also, the results of our investigation may be useful for growers concerning oil yield as well as plant breeders who aim to develop new sunflower genotypes more resistant to heat stress.

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Declaration of competing interest
The authors have declared no competing interests.

Ethical statement
There is no need to obtain permission from the ethics committee for this study.

Authors' Contributions
Ali Doğru designed the study, conducted the study, analyzed the results, and wrote the manuscript. SezenToksoy Köseoğlu helped design the study and analyze the data and reviewed the manuscript.

References

Allakhverdiev, S. I., Kreslavski, V. D., Los, D. A., Carpentier, D., & Mohanty, P. (2008). Heat stress: an overview of molecular responses in photosynthesis. *Photosynthesis Research, 98,* 541-550. 10.1007/s11120-008-9331-0

Ameen, M., Zia, M. A., Alawadi, H. F. N., Naqve, M., Mahmood, A., Shahzad, A. N., Khan, B. A., Alhammad, B. A., Aljabri, M., & Seleiman, M. F. (2024). Exogenous application of selenium on sunflower (*Helianthus annuus* L.) to enhance drought stress tolerance by morphophysiological and biochemical adaptations. *Frontiers in Plant Science, 15,* 1427420. https://doi.org/10.3389/fpls.2024.142420

Binder, B. M., & Patterson, S. (2009). Ethylene-dependent and -independent regulation of abscission. *Stewart Postharvest Reviews, 5,* 1-10.

Biswal, B., Joshi, P. N., Raval, M. K., & Biswal, U. (2011). Photosynthesis, a global sensor of environmental stress in green plants: stress signaling and adaptation. *Current Science, 101,* 47-56.

Camejo, D., Rodriguez, P., Morales, M. A., Dell'amico, J. M., Torrecillas, A., & Alarcon, J. J. (2005). High temperature effects on photosynthetic activity of two tomato cultivars with different heat susceptibility. *Journal of Plant Physiology, 162,* 281-289. 10.1016/j.jplph.2004.07.014

Catiempo, R. L., Photchanachai, S., Bayogan, E. R. V., & Vichitsoonthonkul, T. (2021). Possible role of nonenzymatic antioxidants in hydroprimed sunflower seeds under heat stress. *Crop Science, 161,* 1328-1339. 10.1002/csc2.20403

Chiluwal, A., Bheemanahalli, R., Kanaganahalli, V., Boyle, D., Perumal, R., Pokharel, M., & Jagadish, S. V. K. (2020). Deterioration of ovary plays a key role in heat stress-induced spikelet sterility in sorghum. *Plant Cell and Environment, 43,* 448-462. 10.1111/pce.13673

Debaeke, P., Casadebaig, P., Flenet, F., & Langlade, N. (2017). Sunflower crop and climate change: Vulnerability, adaptation and mitigation potential from case-studies in Europe. *Oilseeds and Fats, Crops and Lipids, 24(1), D102.* https://doi.org/10.1051/ocl/2016052

Deviren, R., & Eryiğit, T. (2017). The determination of yield performance of some sunflower (*Helianthus annuus* L.) cultivars under Iğdır plain irrigable conditions. *KSU Journal of Natural Sciences, 20 (special issue),* 166-171. 10.18016/ksudobil.349185

Doğru, A., & Çakırlar, H. (2020). Is leaf age a predictor for cold tolerance in winter oilseed rape plants? *Functional Plant Biology, 47(3),* 250-262. 10.1071/FP19200

Doğru, A. (2021). Effects of heat stress on photosystem II activity and antioxidant enzymes in two maize cultivars. *Planta, 253,* 85-99.

Drake, J. E., Tjoelker, M. G., Varhammar, A., Medlyn, B. E., Reich, P. B., Leigh, A., & Barton, C. V. M. (2018). Trees tolerate an extreme heatwave via sustained transpirational cooling and increased leaf thermal tolerance. *Global Change Biology*, *24(6),* 2390-2402. 10.1111/gcb.14037

Duncan, D. B. (1955). Multiple range test and multiple F test. *Biometrics, 11(1),* 1-42. http://dx.doi.org/10.2307/3001478

Friedlingstein, P., Houghton, R. A., Marland, G., Hackler, J., Boden, T. A., Conway, T. J., Canadell, J. G., Raupach,

M. R., Ciais, P., & Le Quere, C. (2010). Update on CO_2 emissions. *Nature Geoscience*, *3(12),* 811-812. 10.1038/ngeo1022

Georgieva, K., & Lichtenthaler, H. L. (1999). Photosynthetic activity and acclimation ability of pea plants to low and high temperature treatment as studied by means of chlorophyll fluorescence. *Journal of Plant Physiology*, *155,* 416-423.

Gupta, R. (2020). Manganese repairs the oxygen-evolving complex (OEC) in maize (*Zea mays* L.) damage during seawater vulnerability. *Journal of Soil Science and Plant Nutrition*, *20,* 1387-1396. 10.1007/s42729-020-00220-2

Haider, S., Iqbal, J., Naseer, S., Yaseen, T., Shaukat, M., Bibi, H., Ahmad, Y., Daud, H., Abbasi, N. L., & Mahmood, T. (2021). Molecular mechanisms of plant tolerance to heat stress: current landscape and future perspectives. *Plant and Cell Reports*, *40,* 2247-2271. 10.1007/s00299-021-02696-3

Hoagland, D. R. (1920). Optimum nutrient solutions for plants. *Science*, *52(1354),* 562-564.

Impa, S. M., Raju, B. R., Hein, N. T., Sandhu, J., Prasad, P. V. V., Walia, H., & Jagadish, S. V. K. (2021). High night temperature effects on wheat and rice-Current status and way forward. *Plant Cell and Environment*, *43,* 431-447. 10.1111/pce.14028

Jagadish, S. V. K., Way, D. A., & Sharkey, T. D. (2021). Plant heat stress: Concepts directing future research. *Plant Cell and Environment*, *44,* 1992-2005. 10.1111/pce.14050

Kalaji, M. H., Govindjee, Bosa, K., Koscielniak, J., & Golaszewska, K. Z. (2011). Effects of salt stress on photosystem II efficiency and CO_2 assimilation of two Syrian barley landraces. *Environmental and Experimental Botany*, *73,* 64-72. 10.1016/j.envexpbot.2010.10.009

Kan, Y., Mu, X. R., Gao, J., Lin, H. X., & Lin, Y. (2023). The molecular basis of heat stress responses in plants. *Molecular Plant*, *16,* 1612-1634. 10.1016/j.molp.2023.09.013

Kumar, D., Singh, H., Raj, S., & Soni, V. (2020). Chlorophyll *a* fluorescence kinetics of mung bean (*Vigna radiata L.*) grown under artificial continuous light. *Biochemical and Biophysical Reports*, *24,* 100813. https://doi.org/10.1016/j.bbrep.2020.100813

Laloi, C., Przybyla, D., & Apel, K. (2006). A genetic approach towards elucidating the biological activity of different reactive oxygen species in *Arabidopsis thaliana*. *Journal of Experimental Botany*, *57,* 1719-1724. 10.1093/jxb/erj183

Li, B., Gao, K., Ren, H., & Tang, W. (2018). Molecular mechanisms governing plant responses to high temperatures. *Journal of Integrative Plant Biology*, *609,* 757-779. 10.1111/jipb.12701

Lotfi, R., Ghassemi-Golezani, K., & Pessarakli, M. (2020). Salicylic acid regulates photosynthetic electron transfer and stomatal conductance of mung bean (*Vigna radiata* L.) under salinity stress. *Biocatalysis and Agricultural Biotechnology*, *26,* 101635. 10.1016/j.bcab.2020.101635

Meravi, N., & Prajapati, S. K. (2018). Temporal variation in chlorophyll fluorescence of different tree species. *Biological Rhythym Research*, *49,* 1-7. 10.1080/09291016.2018.1528694

Mittler, R., Finka, A., & Goloubinoff, P. (2012). How do plants feel the heat? *Trends in Biochemical Science*, *37,* 118-125. 10.1016/j.tibs.2011.11.007

Ortiz-Bobea, A., Wang, H., Carillo, C. M., & Ault, T. R. (2019). Unpacking the climatic drivers of US agricultural yields. *Environmental Research Letters*, *14,* 064003. 10.1088/1748-9326/ab1e75

Oukarroum, A., Bussotti, F., Goltsev, V., & Kalaji, M. H. (2015). Correlation between reactive oxygen species production and photochemistry of photosystems I and II in *Lemna minor* L. plants under salt stress. *Environmental and Experimental Botany*, *109,* 80-88. 10.1016/j.envexpbot.2014.08.005

Reich, P. B., Sendall, K. M., Stefanski, A., Rich, R. L., Hobbie, S. E., & Montgomery, R. A. (2018). Effects of climate warming on photosynthesis in boreal tree species depend on soil moisture. *Nature*, *562,* 263-267. 10.1038/s41586-018-0582-4

Ruan, Y. L., Jin, Y., Yang, Y. J., Li, G. J., & Boyer, J.S. (2010). Sugar input, metabolism, and signaling mediated by invertase: roles in development, yield potential, and response to drought and heat. *Molecular Plant*, *3,* 942-955. 10.1093/mp/ssq044

Sehgal, A., Sita, K., & Nayyar, H. (2016). Heat stress in plants: Sensing and defence mechanism. *Journal of Plant Science Research*, *32,* 195-210. https://doi.org/10.3390/agronomy8070128

Sharkey, T. D., & Zhang, R. (2010). High temperature effects on electron and proton circuits of photosynthesis. *Journal of Integrative Plant Biology*, *52,* 712-722. 10.1111/j.1744-7909.2010.00975.x

Villagarcia, L., Were, A., Domingo, F., Garcia, M., & Alados-Arboledos, L. (2007). Estimation of soil boundary-layer resistance in sparse semiarid stands for evapotranspiration modelling. *Journal of Hydrology*, *342,* 173-183. https://doi.org/10.1016/j.jhydrol.2007.05.023

Wise, R. R., Olson, A. J., Schrader, S. M., & Sharkey, T. D. (2004). Electron transport is the functional limitation of photosynthesis in field-grown Pima cotton plants at high temperature. *Plant Cell and Environment*, *27,* 717-724. https://doi.org/10.1111/j.1365-3040.2004.01171.x

Xiaochuang, C., Chu, Z., Lianfeng, Z., Junhua, Z., Hussain, S., Lianghuan, W., & Qianyu, J. (2017). Glycine increases cold tolerance in rice via the regulation

of N uptake, physiological characteristics, and photosynthesis. *Plant Physiology and Biochemistry*, *112,* 251-260. 10.1016/j.plaphy.2017.01.008

Yamamoto, Y. (2016). Quality control of photosystem II: the mechanism for avoidance and tolerance of light and heat stress are closely linked to membrane fluidity of the thylakoids. *Frontiers in Plant Science*, *7,* 1136. https://doi.org/10.3389/fpls.2016.01136

Yılmaz, G., & Kınay, A. (2015). Determination of yield and yield components some sunflower (*Helianthus annuus* L.) varieties in Tokat-Kazova conditions. *Anadolu Journal of Agricultural Science, 30,* 281-286. 10.7161/anajas.2015.30.3.281-286

Zhao, B., Wang, J., Gong, H., Wen, X., Ren, H., & Lu, C. (2008). Effects of heat stress on PSII photochemistry in a cyanobacterium *Spirulina platensis*. *Plant Science*, *175,* 556-564. 10.1016/j.plantsci.2008.06.003