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Boron toxicity impacts on photosystem II photochemical efficiency of sage (*Salvia officinalis*)

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ABSTRACT:
Although boron (B) is an essential element for plants, it becomes toxic in high concentrations. This study was conducted to determine the effects of B toxicity on the photosynthetic performance of sage (*Salvia officinalis*). Twenty-day old cuttings were exposed to toxic B concentrations (2.5, 5, 7.5, and 10 mM) for 20 days. Chlorophyll fluorescence measurements were determined and analysed by the JIP test. The toxic B content led to a gradual decrease in the efficiency of electron transport, the quantum yields, the photosynthetic performances, and the driving force in sage, while causing an increase in the K-band, L-band, and specific and phenomenological energy fluxes. Membrane damage and water loss gradually increased in response to the severity of toxicity levels (-4.3 fold and 19.5% at 10 mM B, respectively). The reductions in the amounts of photosynthetic pigment and photosynthetic activity showed that sage was highly affected by B toxicity, and even increased anthocyanin and flavonoid amounts were unable to alleviate this effect. Exposure to increased B concentrations was associated with the amount of B accumulation in the sage leaves. This dramatic B accumulation in the sage leaves, which are used in herbal teas and food flavourings, can pose a threat to human health depending on the characteristics of the soil in which the sage grows. An evaluation of PSII photochemical efficiency may serve to determine the effects of B toxicity in sage.

Keywords:
chlorophyll fluorescence, fluorescence transient, JIP test, nutrient toxicity, photosynthesis, photosynthetic pigments.

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INTRODUCTION

Boron (B) plays crucial roles in various physio-biochemical processes as a micronutrient in plants. It is essential for photosynthesis, cell wall synthesis, several enzyme activities and nucleic acid and carbohydrate metabolism (Farghaly *et al*. 2021). When present in toxic levels, B may lead to disorders in the physiological processes (e.g. CO_2 assimilation, photosystem II photochemistry, carbohydrate metabolism, and the antioxidant system) in plants (Hua *et al*. 2021). In the soils of arid and semi-arid regions, insufficient leaching of B may cause toxicity naturally (Öz *et al*. 2014). Boron is also introduced into the soil through anthropogenic activities such as mining, fertilization, or irrigation (Hua *et al*. 2021).

Toxic B levels are very destructive to photosynthesis leading to a reduced photosynthetic area and pigment contents, thus resulting in a reduced photosynthetic rate (Wang *et al*. 2011). Photosystem II (PSII) plays a major role in the response of photosynthesis in plants to environmental stresses and thus to B stress (Han *et al*. 2009). Chlorophyll fluorescence (ChlF) measurements are a reliable, non-invasive and powerful tool for the assessment of photosynthetic electron transport and related processes. Moreover, this technique provides detailed information about both the structure and functionality of the PSII reaction centres (Kalaji *et al*. 2016; Ekmekçi *et al*. 2020). ChlF analysis has been used extensively in many studies examining various plant responses under B stress conditions (Han *et*

al. 2009; Landi *et al*. 2013; Öz *et al*. 2014; Ekmekçi *et al*. 2020). The severity of all boron toxicity symptoms varies among genotypes (Brdar-Jokanović 2020). The plant's ability to restrict B uptake and intrinsic tolerance mechanisms can minimize the physiological disturbances caused by B toxicity (Simón *et al*. 2013). It is known that B toxicity induces the formation of large amounts of reactive oxygen species (ROS) such as superoxide radical ($O_2^{\bullet -}$), hydroxyl radical ($OH^{\bullet}$), and hydrogen peroxide (H_2O_2), which can cause cell membrane damage and oxidative stress, leading to cell death (Molassiotis *et al*. 2006). Enzymatic and non-enzymatic antioxidants (e.g. catalase, superoxide dismutase, peroxidase, ascorbate, and flavonoids) have important functions in the protection of plants against ROS-induced oxidative cellular injury (Çatav *et al*. 2022). Flavonoids and anthocyanins are one of the ROS scavenging components which increase the antioxidant potential of plants (Landi *et al*. 2013). Moreover, Landi *et al*. (2014) mentioned three possible mechanisms through which anthocyanins might alleviate the effects of B toxicity: 1) anthocyanins might chelate B ions and isolate them in the cell vacuole; 2) antocyanins, as extremely potent antioxidants, may reduce the oxidative load; 3) anthocyanins may lessen the generation of ROS by absorbing part of the light energy and thus protect photosynthetic pigments from photodamage. Flavonoids, plant secondary metabolites, have free radical suppressing activity as a hydrogen donor leading to a reduction in ROS once it is produced (Zhang *et al*. 2017; Farghaly *et al*. 2021).

Sage (*Salvia officinalis* L.) is a perennial woody sub shrub belonging to the Mediterranean region which is cultivated all over the world. In addition to being a medicinal plant containing various antioxidant compounds, sage is also used in the perfumery and food industries (Taârit *et al*. 2012). Moreover, dried sage leaves are consumed as food flavouring and as herbal tea (Bettaieb *et al*. 2009). In the literature, most of the studies have focused on the antioxidant capacity, phenolic content and/or essential oil composition of sage under various stress conditions (Lu & Foo 2001; Hendawy & Khalid 2005; Taarit *et al*. 2010, 2012; Bettaieb *et al*. 2011). There remains a lack of information about the photosynthetic response of the sage plant to B stress. Therefore, in this research sage is used to study high B toxicity conditions, photochemical activity evaluated by ChlF measurements, pigment and water contents, membrane integrity and the accumulation of B in the leaves. The aim of this study was 1) to understand the tolerance level of sage in response to different B toxicity levels; 2) to investigate the B tolerance by polyphasic fluorescence kinetics; 3) to determine the B accumulation levels of sage leaves; and 4) to elucidate possible physiological mechanisms in terms of the photosynthetic process in sage under B toxicity conditions.

MATERIALS AND METHODS

The sage plants were propagated by cutting the mother plants obtained from a plant nursery. The stems (10 cm) with two nodes and four opposite leaves were cultivated in 1 L pods filled with distilled water for 15 days in a controlled growth chamber at 25 ± 1°C with a 16 h photoperiod at 40 ± 5% humidity and 250 µmol m^{-2} s^{-1} light intensity until the adventive roots emerged. The rooted cuttings continued to grow in half strength Hoagland's transferred to sterile hydroponic cultures for B treatments, containing four different boron (H_3BO_3) concentrations (2.5 mM, 5 mM, 7.5 mM, and 10 mM) for another 20 days. The control plants were transferred to half strength Hoagland's solution without extra H_3BO_3. The control and B treatment solutions were renewed every 2 days.

Chlorophyll fluorescence (ChlF) measurements were performed using the Handy PEA (Hansatech Instruments Ltd., Norfolk, UK) fluorimeter on selected fully expanded leaves. Following a 30 min dark adaptation, the samples were illuminated with continuous light (650 nm peak wavelength; 3000 µmol (photon) m^{-2} s^{-1} maximum light intensity for 1 s) provided by three LEDs and the fast fluorescence kinetics (F_0 to F_M) were recorded (Strasser *et al*. 2004). Photoinduced chlorophyll fluorescence transients (OJIP) were used to calculate the JIP-test parameters described in Table 1.

The photosynthetic pigments were extracted from the leaf samples (0.1 g) in 100% acetone and the absorbance of the extracts was measured at 470, 644.8 and 661.6 nm. The content (mg g^{-1} FW) of chlorophyll (Chl) (*a*+*b*) and carotenoid (Car) (x+c) was calculated using adjusted extinction coefficients (Lichtenthaler 1987). The anthocyanins were extracted from the leaf samples in 1 ml of acidified methanol [methanol:water:HCl (79:20:1)] for 48 h at 4°C. The absorbance was measured at 530 and 657 nm. The anthocyanin content was calculated according to Mancinelli *et al*. (1975) and expressed as mg g^{-1} FW. The flavonoid content of the leaves was determined using the method of Mirecki & Teramura (1984). Samples from the leaves (0.1 g each) were extracted in 6 ml acidified methanol [methanol:water:HCl (79:20:1)]. The extract was centrifuged and the supernatant was diluted 1:10 in acidic methanol. The relative flavonoid content (A_{300}) was estimated from the absorbance at 300 nm of the acidified methanol leaf extracts and calculated as the percentage of the control plants (C).

The relative leakage ratio (RLR) was measured indirectly as the leakage of UV-absorbing substances using the protocol described by Redmann *et al*. (1986) with minor modifications. Five discs of leaf samples (R=0.5 cm) were gently shaken in 10 ml of distilled water for 24 h and the absorption was subsequently measured at 280 nm (A_{280}). After being treated in liquid nitrogen for 20 min, the leaf discs were again gently shaken in incubation water for another 24 h and measured at 280 nm

Table 1. Definition of some of the analysed JIP-test parameters (Strasser *et al*. 2004, 2010). PSI, PSII, RC, CS, and Q_A are for photosystem I, photosystem II, active PSII reaction centres, the cross section of PSII, and the first plastoquinone electron acceptor of PSII, respectively.

	Description
Extracted and technical fluorescence parameters	
F_0	Initial fluorescence intensity, when all PSII RCs are open
F_{300}	Fluorescence intensity at 300 μs
F_J	Fluorescence intensity at the J-step (at 2 ms)
F_I	Fluorescence intensity at the I-step (at 30 ms)
F_M	Maximal fluorescence intensity, when all PSII RCs are closed
F_V	$F_M - F_0$, Maximum variable fluorescence
V_{OJ}	$(F_J - F_0)/(F_M - F_0)$, relative variable fluorescence at the J-step (2 ms)
V_{IP}	$(F_I - F_0)/(F_M - F_0)$, relative variable fluorescence at the I-step (30 ms)
V_{OK}	$(F_{300} - F_0)/(F_M - F_0)$, relative variable fluorescence at the K-step (300 μs)
M_0 or $(dV/dt)_0$	$4(F_{300} - F_0)/(F_M - F_0)$, approximated initial slope (in ms^{-1}) of the fluorescence transient V = f(t)
Efficiencies and quantum yields	
φ_{P0} or TR_0/ABS	$1 - F_0/F_M$ or F_V/F_M, maximum quantum yield of primary photochemistry at t = 0
φ_{E0} or ET_0/ABS	$(1 - F_0/F_M) \times \psi_{E0}$, quantum yield for electron transport at t = 0
ψ_{E0} or ET_0/TR_0	$1 - V_J$, probability (at t = 0) that a trapped exciton moves an electron into the electron transport chain beyond Q_A^-
δ_{R0} or RE_0/ET_0	$(1 - V_I)/(1 - V_J)$, the efficiency with which an electron can move from the reduced intersystem electron acceptors to the PSI end final electron acceptors
φ_{R0} or RE_0/ABS	$\varphi_{P0} \times \psi_0 \times \delta_{R0}$, the quantum yield of electron transport from Q_A^- to the PSI end electron acceptors
φ_{D0} or DI_0/ABS	Quantum yield of energy dissipation at t = 0
Specific energy fluxes (per active PSII)	
ABS/RC	$M_0 \times (1/V_J) \times (1/\varphi_{P0})$, apparent antenna size of an active PSII
TR_0/RC	$M_0 \times (1/V_J)$, maximum trapped exciton flux per active PSII
ET_0/RC	$M_0 \times (1/V_J) \times \psi_{E0}$, the flux of electrons transferred from Q_A^- to PQ per active PSII
DI_0/RC	ABS/RC – TR_0/RC, the flux of energy dissipated in progresses other than trapping per active PSII
Phenomenological energy fluxes (per CS)	
ABS/CS_0	F_0, absorbed photon flux per excited CS
TR_0/CS_0	$\varphi_{P0} \times (ABS/CS_0)$, maximum trapped exciton flux per CS
ET_0/CS_0	$\varphi_{E0} \times (ABS/CS_0)$, the flux electrons from Q_A^- to PQ per CS
Performance indexes	
PI_{ABS}	$(RC/ABS) \times [\varphi_{P0}/(1 - \varphi_{P0})] \times [\psi_{E0}/(1 - \psi_{E0})]$, performance index for energy conservation from exciton to the reduction of intersystem electron acceptors
PI_{TOTAL}	$PI_{ABS} \times [\delta_{R0}/(1 - \delta_{R0})]$, performance index for energy conservation from exciton to the reduction of PSI end electron acceptors
Driving force	
DF_{ABS}	$\log(PI_{ABS})$, driving force on absorption basis

(A_{280}'). The RLR was calculated according to the A_{280}/A_{280}' formula. The water status of the leaves was evaluated by calculating the percentage of relative water content (RWC) as: RWC (%) = [(FW – DW)/(SW – DW)] × 100, where FW is the fresh weight, DW is the dry weight and SW is the water-saturated weight (Farrant 2000).

The leaf tissues were dried at 80°C for 48 h and 0.2 g of the dried samples were ashed at 500°C for 5 h and dissolved in 0.1 N HNO_3. The B content (mg kg^{-1} DW) was quantified using inductively coupled plasma mass spectrometry (ICP-MS, Agilent, 7700, USA).

The experiment was performed in a completely randomized design with 3 replicates for each treatment and the differences in the measured variables between the treatments were analysed by ANOVA and according to the least significant difference (LSD) at the 5% level. All the analyses were performed using SPSS v. 20.0, Inc, Chicago, IL, USA.

RESULTS AND DISCUSSION

Boron is involved in many physiological processes related to plant growth. However, toxic B can lead to the decreased growth, photosynthetic inefficiencies and membrane integrity of plants (Moustafa-Farag *et al.* 2020). In addition, at toxic levels, B inhibits photosynthesis by causing the structural degradation of thylakoids, changing the electron transport rate and/or affecting the activities of enzymes involved in photosynthesis (Ekmekçi *et al.* 2020). In order to monitor the successive steps of the excitation energy transformation, ChlF parameters (Table 1) were used to obtain the effect of excess B levels on the photosynthetic efficiency of sage. Each B toxicity level has a gradual significant effect on all the ChlF parameters. The parameters representing the relative values of the control are represented by spider plot graphics (Fig. 1). Exposure to B caused an increase in both V_{OK} and V_{OJ}, indicating the change in the L- and K- bands, respectively, while the V_{IP} values of all the treatments declined (Fig. 1A). The highest L- and K- band values were determined in the 10 mM B treatment, 1.6- and 1.2-fold of control, respectively, indicating the inactivation of the oxygen-developing complex which caused an incompatibility between the acceptor and donor side of PSII (Oukarroum *et al.* 2007). The decreased V_{IP} values were more pronounced for the highest B concentration treatment (48%). Ekmekçi *et al.* (2020) found that the decrease in V_{IP} in response to the toxic B treatments may be related to the re-reduction of plastocyanin and $P700^+$ and/or a decreased electron flux towards cyclic electron flow and/or lowered electron transfer efficiency towards the PSI end electron acceptors and/or a decline in PSI content. The efficiency and quantum yield parameters were affected differently by the applied boron levels (Fig. 1A). The results show that the changes of the ψ_{E0}, φ_{P0}, δ_{R0} and φ_{E0} parameters for the 2.5 mM B treatment were not statistically significant, where the 10 mM B treatment resulted in the greatest variation among the parameters. Although it is known that φ_{P0} is a good indicator of PSII photoinhibition, photoinhibition is considered to be more accurately described by an increase in DI_0/RC and

Table 2. The Chl *a*+*b* (mg g^{-1} FW), Car (mg g^{-1} FW), Anthocyanin (mg g^{-1} FW), Flavonoid (%) and B (mg kg^{-1} DW) contents of the sage leaves exposed to B. C represents 40 day old control plants. Means ±SEs, *n*= 6 (for Chl and Car) or 3 (for Anthocyanin and B). Different letters indicate significant difference at $P < 0.05$ according to LSD 5%.

	Parameters				
Treatments	**Chl *a*+*b***	**Car**	**Anthocyanin**	**Flavonoid**	**B**
C	0.075 ±0.001[a]	0.016 ±0[a]	0.0046 ±0[a]	100	0.1 ±0.002[a]
2.5 mM	0.056 ±0.001[b]	0.009 ±0[b]	0.0052 ±0[b]	147	4.3 ±0.197[b]
5 mM	0.049 ±0.001[c]	0.006 ±0[c]	0.0061 ±0[c]	163	10.2 ±0.111[c]
7.5 mM	0.034 ±0.002[d]	0.006 ±0[c]	0.0064 ±0[c]	189	24.8 ±0.103[d]
10 mM	0.028 ±0.001[e]	0.005 ±0[d]	0.0072 ±0[d]	219	40.4 ±0.220[e]
LSD 5%	0.004	0.001	0.0004		0.7

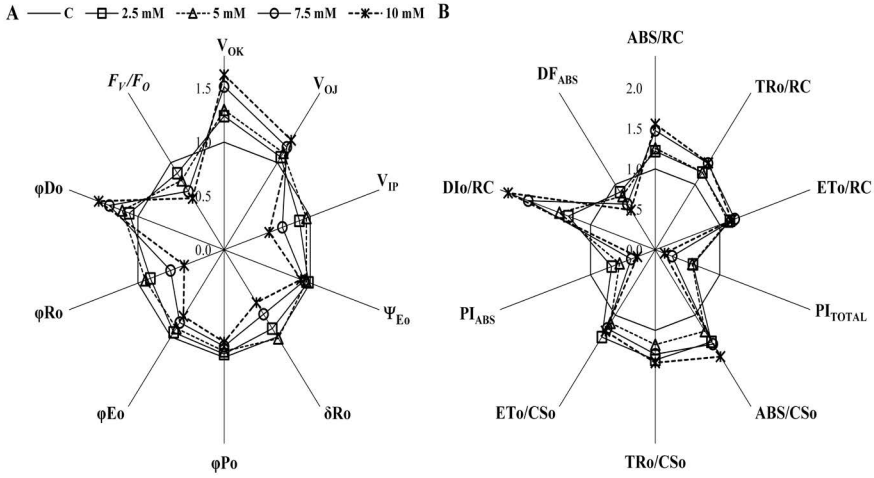

Fig. 1. The radar-plot presentation of selected JIP test parameters quantifying the efficiencies and quantum yields **A**) and specific and phenomenological energy fluxes; **B**) of dark-adapted sage leaves exposed to B toxicity of 2.5, 5, 7.5, and 10 mM H_3BO_3 treatment. The mean values of the parameters were plotted relative to their respective control values (n = 6).

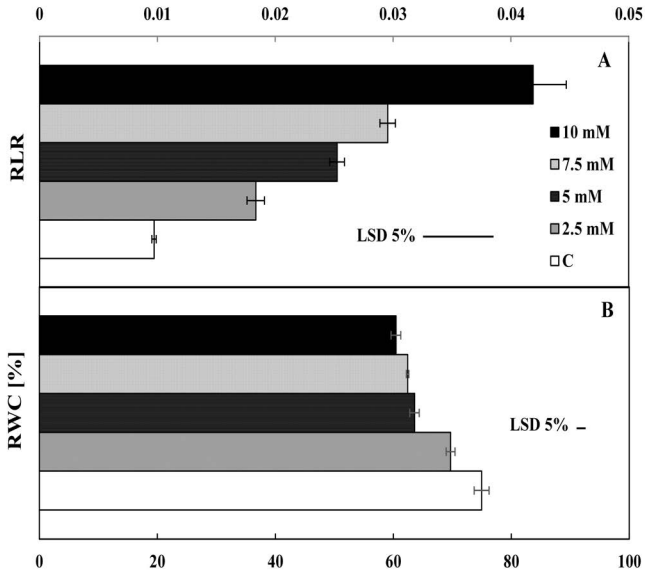

Fig. 2. **A**) Relative Leakage Ratio (RLR), and **B**) Relative Water Content (RWC) of the sage leaves exposed to 2.5, 5, 7.5, and 10 mM H_3BO_3 treatments. C represents 40 day old control plants. The error bars represent the standard error (± SE) for three (RLR) and six (RWC) replicates.

a decrease in ψ_{E0} (Han *et al*. 2009). The value of ψ_{E0} referring to the reduction of electron transport in PSII gradually decreased by 5%, 7% and 11% is response to the 5 mM, 7.5 mM and 10 mM B treatments, respectively. Highly toxic B concentrations (7.5 and 10 mM) caused a dramatic fall decrease in δ_{R0} (26 and 40%, respectively), indicating a decline in electron transport between the PSI and PSII. Among the φ_{P0} (the quantum yields of photoinduced electron transfer from P680 to Q_A), φ_{E0} (from Q_A^- to PQ), and φ_{R0} (from PQ to the PSI electron acceptors) parameters, φ_{R0} showed the highest decrease for all the B treatments. Han *et al*. (2009) emphasized a decline in F_V along with an increase in F_0 as the main characteristic of inhibition of the PSII acceptor side. Likewise, the F_V/F_0 results were gradually reduced by increased B concentrations.

The specific energy fluxes per active PSII parameter (ABS/RC, TR_0/RC, ET_0/RC, and DI_0/RC) increased with the B treatments (Fig. 1B). An approximately 1.5-fold increase was determined at highly toxic B concentrations in ABS/RC, indicating the reduction of effective antenna size. Moreover, the maximum trapping rate of PSII (TR_0/RC) of the B treated leaves exhibited a similar pattern with ABS/RC. The decrease in active PSII reaction centres may be related to a decline in the photosynthetic pigment contents of the B treated sage (Table 2). The increment in the energy dissipation parameters (φ_{D0} and DI_0/RC) was more pronounced for the 10 mM B treatment, 1.5- and 2.3-fold for the corresponding control, respectively (Fig. 1). The increased values of φ_{D0} and DI_0/RC demonstrated that the trapped energy probably dissipated as heat and the connection between the systems was lost (Strasser *et al*. 2010). The phenomenological energy flux parameters (ABS/CS_0, TR_0/CS_0, and ET_0/CS_0) exhibited similar behaviour when compared with the control under the B treatments (Fig. 1B). Toxic B concentrations (7.5 and 10 mM) led to the enhancement of the parameters, marked in ABS/CS_0 (1.4- and 1.6-fold of the control, respectively). The performance indexes, PI_{ABS} and PI_{TOTAL}, showed significant decreases in response to all the B toxicity levels (Fig. 1B). In order to quantify the PSII behaviour, PI_{ABS} is used to express energy absorption, trapping and conversion into the electron transport steps. However, PI_{TOTAL} includes additional electron steps to PI_{ABS} and refers to a measure of the performance up to the reduction of PSI end electron acceptors (Kalaji *et al*. 2014). The gradual decline of PI_{ABS} and PI_{TOTAL} showed that B toxicity reduces the electron transport capacity and thus photosynthetic performance in all the treatments. The reductions were more pronounced at the highest toxic level for PI_{ABS} and PI_{TOTAL} (78 and 86%, respectively). The effect of B toxicity on the DF_{ABS} of photosynthesis was similar to the performance indexes and sharp declines were determined at high toxic concentrations (7.5 and 10 mM) (Fig. 1B).

The deterioration of photosynthesis could be attributed to the decrease in the electron transport rate, declined CO_2 use efficiency, and damage to the photosystem II machinery due to a decline in photosynthetic pigments (Day & Aasim 2020). Similarly, according to the results of this research, the decreases in photosynthetic activity were accompanied by a decline in the pigment contents of the B treated leaves (Table 2). While gradual reductions occurred in the Chl (*a*+*b*) content with increasing B concentrations, the Car contents declined sharply until 5 mM B and then slight changes were determined at 7.5 and 10 mM treatments. Although Car is known to be one of the protectors of the photosynthetic apparatus from photodamage, this mechanism did not function in this study. B toxicity-induced chlorophyll and carotenoid deficiency was also determined in watermelon leaves (Moustafa-Farag *et al*. 2020). In contrast to Chl and Car, the anthocyanin and flavonoid contents rose significantly with B toxicity levels (Table 2). However, the decreased photosynthetic efficiency of sage under B toxicity showed that the light screening role of anthocyanins was not sufficient to prevent the overexcitation of chloroplasts. Anthocyanins and flavonoids, which are other stress protectors, have antioxidant roles in addition to protecting chlorophyll from photoinhibition in mesophyll cells when chloroplast functionality has been compromised by B toxicity (Landi *et al*. 2014).

Unfortunately, the decreased photosynthetic efficiency (Fig. 1) and increased RLR (Fig. 2A) results show that with increasing B concentrations the increased con-

tents of these protective pigments were unable to protect the leaves from photoinhibition and membrane damage. These results show that although these mechanisms played a role in the attempt to reduce ROS production, the amount of ROS formed exceeded the defence barrier. Moreover, treatment with increasing concentrations of B resulted in the increased accumulation of B by sage (Table 2), which is in agreement with earlier studies showing that the supply of exogenous B determines the B levels in pears (Wang *et al*. 2011), wheat (Öz *et al*. 2014), citrus fruits (Han *et al*. 2009), and sunflowers (Ekmekçi *et al*. 2020).

Toxic B levels led to a dramatic increase in the RLR ratio indicating electrolyte leakage from the sage leaf cells for all the treatments, especially at 10 mM with a 4.3-fold increase in the control (Fig. 2A). B accumulation is reported to be the main determinant of the induction of leaf damage and Landi *et al*. (2013) observed a positive and significant correlation between B accumulation and membrane integrity. The RWC values of the sage also declined significantly with exposure to different B levels (Fig. 2B). The B treatments caused a 7, 15, 17, and 19.5% reduction in RWC in response to exposure to 2.5, 5, 7.5, and 10 mM concentrations of B respectively. Increased electrolyte leakage followed by decreased water content is an indicator of decreased membrane integrity. Since the water loss of the leaves impairs both membrane structure and function, the deterioration of PSII photochemical activity and photosynthetic efficiency in sage is the result of B toxicity.

CONCLUSION

The results of the study point out that B toxicity had a deleterious effect on the physiological mechanisms of sage, even at the lowest level of toxicity treatment. However, the difference in the toxicity levels is particularly evident in the PSII photosynthetic efficiency and, accordingly, in the amount of chlorophyll. The ChlF results indicate that B toxicity caused the inactivation of the oxygen-developing complex (V_{OK} and V_{OJ}), a decline in electron transport between PSI and PSII (δ_{R0}), increased energy dissipation (φ_{D0} and DI_0/RC) and reduced the performance indexes (PI_{ABS} and PI_{TOTAL}). Despite the increase in the anthocyanin and flavonoid contents, which are powerful antioxidants, the significant oxidative load due to decreased photochemical activity led to membrane damage and water loss, indicating that cellular integrity could not be preserved in the B toxicity treated sage leaves. Sage might be evaluated as a promising accumulator due to the increased B accumulation of the leaves and B transport and accumulation should be determined in further studies by investigating its mobility in all the plant organs. Since sage leaves are commonly consumed as herbal tea and food flavouring, it is important for human health to analyse their content before offering them to the consumer.

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Uticaj toksičnosti bora na fotohemijsku efikasnost fotosistema II kod žalfije (*Salvia officinalis*)

Özlem Arslan

Iako je bor (B) je esencijalni element za biljke, u visokim koncentracijama postaje toksičan. Ova studija je sprovedena da bi se utvrdili efekti toksičnosti B na fotosintetske performanse žalfije (*Salvia officinalis*). Dvadeset dana stari klijanci su bile izloženi toksičnim koncentracijama B (2.5, 5, 7.5 i 10 mM) tokom 20 dana. Merenja fluorescencije hlorofila su određena i analizirana JIP testom. Toksični sadržaj B doveo je do postepenog smanjenja efikasnosti transporta elektrona, kvantnih prinosa, fotosintetskih performansi i pokretačke sile kod žalfije, dok je prouzrokovao povećanje K-opsega, L-opsega i specifičnih i fenomenoloških energetskih fluksova. Oštećenje membrane i gubitak vode postepeno su se povećavali sa ozbiljnošću nivoa toksičnosti (-4,3 puta i 19,5% pri 10 mM B, respektivno). Dok je smanjenje količine fotosintetskog pigmenta i fotosintetičke aktivnosti pokazalo da je žalfija jako pogođena toksičnošću B, čak ni povećane količine antocijanina i flavonoida nisu mogle da ublaže ovaj efekat. Izloženost povećanim koncentracijama B je bila povezana sa količinom akumulacije B u listovima žalfije. Ova dramatična akumulacija B u listovima žalfije, koja se koristi kao biljni čaj i aroma za hranu, može ugroziti ljudsko zdravlje u zavisnosti od karakteristika zemljišta na kojem raste. Procena fotohemijske efikasnosti PSII može se koristiti za određivanje efekata toksičnosti B u žalfiji.

Ključne reči: fluorescencija hlorofila, prolazna fluorescencija, JIP test, toksičnost nutrijenata, fotosinteza, fotosintetski pigmenti