ACTA SCIENTIARUM POLONORUM
Acta Sci. Pol. Hortorum Cultus 22(4) 2023, 91-103
https://czasopisma.up.lublin.pl/index.php/asphc ISSN 1644-0692 e-ISSN 2545-1405 https://doi.org/10.24326/asphc.2023.5007
ORIGINAL PAPER
Accepted: 20.03.2023
Issue published: 31.08.2023

COMBINED EFFECTS OF EXCESS BORON AND SALINITY ON THE GROWTH AND IONIC IMBALANCE OF LAVANDIN (*Lavandula* × *intermedia*) PLANT

Halil Samet [1]✉, Yakup Çikili [2], Aysun Çavuşoğlu [3]

[1] Department of Crop and Animal Production, Izmit Vocational School, Kocaeli University, Arslanbey Campus 41280 Kartepe, Kocaeli, Turkiye

[2] Department of Soil Science and Plant Nutrition, Faculty of Agriculture, Çanakkale Onsekiz Mart University, Terzioğlu Campus 17100 Çanakkale, Turkiye

[3] Department of Plant Protection, Faculty of Agriculture, Kocaeli University, Arslanbey Campus 41280 Kartepe, Kocaeli, Turkiye

ABSTRACT

Generally, moderate to high salinity conditions and excess boron (B) occur together as limiting factors for plant growth in the soils of arid and semiarid regions. To determine the combined effect of excessive boron, salinity stress, or both, five different levels of B (0, 0.3, 0.6, 1.2, and 1.8 mM) and 80 mM sodium chloride (NaCl) were applied to lavandin plants grown in a greenhouse. The results showed that under nonsaline conditions, biomass production in shoots and roots and photosynthetic pigment contents (chlorophyll (Chl) *a*, *b*, and Chl *a* + *b*) decreased with exceptionally high B applications compared to the control. Moreover, the bioconcentration (BCF) of B (in shoots and roots), potassium (K) concentrations (in roots), K/sodium (Na) and calcium (Ca)/Na ratios (in shoots), and Ca/B ratios (in shoots and roots) decreased for all B applications compared to the control. In contrast, all B applications caused a remarkable increase in the carotenoid (Car)/Chl ratio, B concentrations (in shoots and roots), translocation (TF) of B, and net B accumulation compared to the control. In addition, under nonsaline conditions, concentrations of K (in shoots), Ca (in shoots and roots), and K/Na and Ca/Na ratios (in roots) were significantly increased by B applications compared with the control. Under saline conditions, significant decreases in Chl *b*, Chl *a* + *b*, BCF of B (in shoots and roots), and Ca/B ratio (in shoots) were observed in all B applications compared to the control. However, under saline conditions, B application caused significant increases in the Car/Chl ratio, TF of B, net B accumulation, and concentrations of B (in shoots and roots), K (in shoots), Ca, and Na (in shoots and roots) compared to the control. It was concluded that although it is not seen in the growth parameters, NaCl application could effectively alleviate the harmful effects of B toxicity in lavandin plants. Under saline conditions, notable decreases in the mean B concentration in shoots could be strong evidence for this hypothesis.

Key words: Biomass, boron toxicity, chlorophyll, ion accumulation, *Lavandula hybrida*, NaCl-salinity

INTRODUCTION

Although B is an essential element for plant growth and plays a crucial role in many physiological processes [García-Sánchez et al. 2020], toxic concentrations are a significant stress factor limiting crop yields, and it may be easy to reach toxic B concentrations in arid and semiarid regions due to evaporation from groundwater containing high levels of B and accumulation in the topsoil [Tanaka and Fujiwara 2008]. Furthermore, soil toxic B levels can increase with anthropogenic activities, such as B-related mining and processing,

✉ halilsamet@yahoo.com

fertilization, or irrigation [Parks and Edwards 2005]. Excess B disrupts plant physiological processes and consequently results in visual symptoms such as chlorosis and necrosis of leaves [Han et al. 2009].

Salinity is an abiotic stress factor that occurs because of high concentrations of soluble salts in the rooting medium and negatively affects crop yield [Cordovilla et al. 2014]. This stress negatively affects plant roots in two ways. The first is osmotic stress, caused by low water potential in the root zone. The second is ionic stress, which is caused by the variability of the concentration of specific ions within the rooting medium [Berntein and Kafkafi, 2002]. A decrease in osmotic potential in the root zone restricts water absorption from the rooting medium and, thus, the uptake of nutrients dissolved in soil water. Ion imbalance in the rooting medium is another salinity result and is usually caused by uptake competition between Na and K ions; the uptake of Ca and Mg ions can also be inhibited in saline conditions [Franco et al. 2011a].

The combined effects of B toxicity and salinity stress co-occurring in arid and semiarid areas have recently attracted the attention of researchers [García-Sánchez et al. 2020]. Pandey et al. [2019] recommended that B and salinity stress should be evaluated as a new stress factor named BorSal. They also indicated that this new stress factor could affect most physiological activities, such as photosynthesis, transpiration, ionic mobility, and water transport. Javid et al. [2014] reported that the responses of plants to individual stresses originating from excess B and salinity and their responses to the BorSal stress factor were different, and it would be a more accurate approach to evaluate the effects of BorSal in Brassica species. In another study using rice plants, there was a decrease in plant growth and biomass production with the application of NaCl (10 dS m^{-1}) and B (2.5 mg kg^{-1}) [Farooq et al. 2019]. On the other hand, Carmassi et al. [2013] stated that irrigation water enriched with B increased B accumulation in tomato leaves 35–40 days after planting. In contrast, NaCl and B concentrations in irrigation water had fewer adverse effects on leaf area development, biomass accumulation, crop yield, and fruit quality. It has also been reported that salinity stress reduces the transpiration rate of plants, thereby restricting the uptake and transport of B [Yermiyahu et al. 2008].

As summarized above, the combined or individual effects of salinity and excess B on plant growth and yield have been investigated in many plants, but there are limited studies on the effects of these factors on the behavior or accumulation of ions. This study focuses on the response of the lavandin plant to toxic B levels under saline conditions. We also aimed to determine the interactions between salinity and B on lavandin performance, including growth parameters, concentrations, and accumulations of ions.

MATERIAL AND METHODS

Growing conditions and experimental design

This study, carried out with lavandin (*Lavandula* × *intermedia* Emeric ex Loisel syn. *L. hybrida*, a hybrid of *L. angustifolia* and *L. latifolia*), was conducted during the summer season in a greenhouse with an average temperature of 26°C/17°C (day/night) and an average relative humidity of 65%.

Four-month-old lavandin saplings were procured from a private company that produces outdoor ornamental plants and transferred to polyethylene containers with a capacity of 2 liters (one plant each), filled with perlite, at ambient temperature in the greenhouse environment. Before the experiment, the saplings were watered with different rates of modified Hoagland solution for acclimatization for 12 days (four days quarter strength, four days half strength, and four days full strength). This solution contains 5 mM calcium nitrate tetrahydrate [$Ca(NO_3)_2 \cdot 4H_2O$], 5 mM potassium nitrate (KNO_3), 2mM magnesium sulfate heptahydrate ($MgSO_4 \cdot 7H_2O$), 1mM potassium dihydrogen phosphate (KH_2PO_4), 45.5 µM boric acid (H_3BO_3), 44.7 µM iron sulfate heptahydrate ($FeSO_4 \cdot 7H_2O$), 30.0 µM sodium chloride (NaCl), 9.1 µM manganese sulfate monohydrate ($MnSO_4 \cdot H_2O$), 0.77 µM zinc sulfate heptahydrate ($ZnSO_4 \cdot 7H_2O$), 0.32 µM copper sulfate pentahydrate ($CuSO_4 \cdot 5H_2O$), 0.10 µM ammonium molybdate tetrahydrate [$(NH_4)_2Mo_7O_{24} \cdot 4H_2O$], and 54.8 µM disodium EDTA dihydrate ($Na_2EDTA \cdot 2H_2O$). During the experimental period, the pH of the nutrient solution was adjusted to 6.5 with dilute hydrochloric acid (HCl), sodium hydroxide (NaOH) solutions, or both.

To study the combined effect of increasing B and NaCl salinity, samples were exposed to five B appli-

cations (0, 0.3, 0.6, 1.2, and 1.8 mM B as H_3BO_3) and two salinity applications (0 and 80 mM NaCl). These levels were dissolved separately in a full-strength modified Hoagland solution in different containers, and during the experiment, the plants were irrigated with these solutions (100 mL per day). The B levels were chosen based on previous studies and their differentiated toxic levels for various plant species.

Sampling and harvesting of plants

Lavandin plants were harvested after 42 days and separated into shoots and roots to determine the fresh and dry weights of the biomass. The shoots were weighed, and the roots were carefully separated from the soil and dipped into an aerated 0.5 mM calcium chloride (CaC_{l2}) solution for 15 min to eliminate adsorbed nutrients from the root surface. The roots were washed three times with running tap water and rinsed with deionized water to remove any particles attached to the plant surfaces. Then, all the samples were dried in an air-forced oven at 70°C until a constant mass was reached. After cooling to room temperature, they were weighed for the shoot, root dry weights, and ground to powder for nutrient ion analysis.

Determination of bioconcentration, translocation, and accumulation

The capacity of the lavandin plant to accumulate B was evaluated based on the bioconcentration factor (BCF), the translocation factor (TF), and the net ion accumulation via roots. The BCF, which is an essential parameter for ion toxicity and risk assessment [Burkhard et al. 2012], was defined as the ratio of the total B concentration in the root or shoot to the B concentration in the rooting medium [Moradi and Ehsanzadeh 2015]. It was calculated for both the shoots and roots. The TF level is defined as the ratio of B concentration in the shoot to that in the root [Cikili et al. 2016]. The net ion accumulation via roots was the rate of total ion amounts in the whole plant to root DW [Cikili et al. 2016]. The last two values have been calculated by equations [1] and [2], respectively [Moradi and Ehsanzadeh 2015].

[1] TAR of B ($\mu g\ g^{-1}$ DW day^{-1}) =

$= ([B]_{shoot} \times DW_{shoot}) +$

$+ ([B]_{root} \times DW_{roo}t)/\text{growth day} \times$

$\times (DW_{shoot} + DW_{root})$

[2] Net ion accumulation via roots ($\mu g\ g^{-1}$ DW) =

= total amount of ion in whole plant (μg)/DW_{root}

where [B] shoot or root is B concentration in shoot or root.

Determination of photosynthetic pigments

The contents of photosynthetic pigments (Chl *a*, *b*, and Car) were measured in the freshest and youngest fully expanded leaves just before harvest. The samples (250 mg) taken out of plants were cut into small pieces and homogenized in 10 mL of acetone (90% v/v) with a homogenizer (Heidolph DIAX 900, Kelheim, Germany). The homogenate was filtered, and the absorbance of the extract was determined at 663, 645, and 470 nm using a spectrophotometer (Shimadzu UV-1201, Japan). The pigment contents were calculated according to Lichtenthaler [1987].

Determination of nutrient elements

For the measurement of nutrient ion concentrations, 500 mg of each of the shoot samples was dry-ashed in a muffle furnace at 500°C for 6 h, and then the cooled ash was dissolved in a 10 N nitric acid (HNO_3) solution [Miller 1988]. The B and phosphorus (P) concentrations were measured using a spectrophotometer (Shimadzu UV-1201, Japan). The potassium (K), calcium (Ca), and sodium (Na) concentrations were analyzed using a flame photometer.

Calculation of percentage changes

Percentage changes in the investigated parameters represented increases or decreases compared to the control group (B-free or NaCl-free) and were calculated by equation [3].

[3] The change (%) = 100 × [(The value obtained with the application of B or NaCl – The value obtained with the control group)/The value obtained with the control group]

Statistical analysis

The experiment was designed as a completely randomized factorial design with three replicates, and the obtained data were analyzed using ANOVA with the MINITAB package program (Minitab Corp., State College, PA). Duncan's Multiple Range Test (DMRT) at the significance level ($\alpha = 0.05$) was used to compare application differences. The significance levels are represented by * at $p < 0.05$, ** at $p < 0.01$, *** at $p < 0.001$, and ns – nonsignificant.

RESULTS

Plant growth

A notable interaction between NaCl and B stress was observed in the biomass production of the lavandin plant (Table 1). Under nonsaline conditions, low B applications (0.3 and 0.6 mM) caused insignificant increases in shoot and root FW and DW compared to the control (B-free). However, high B applications (1.2 and 1.8 mM) significantly decreased the shoot FW by 13.0% and 39.8%, respectively. The same B applications caused a significant decrease in the root FW (28.0% and 55.6%, respectively), shoot DW (14.9% and 32.4%, respectively), and root DW (16.3% and 38.7%, respectively). Under nonsaline conditions, the effect of B application on the shoot-to-root ratio and root length was insignificant (Tab. 1).

Under saline conditions, the effects of B treatments on lavandin biomass production were insignificant (Tab. 1). However, the B levels applied under saline conditions caused notable reductions compared to those applied under nonsaline conditions. The 0.3, 0.6, 1.2, and 1.8 mM B applications caused significant decreases in shoot FWs at 62.7%, 60.1%, 41.2%, and 27.5%, respectively. Likewise, the same applications caused significant reductions in root FWs at 74.4%, 70.6%, 46.0%, and 29.8%, respectively (Tab. 1).

Photosynthetic pigments

Under both nonsaline and saline conditions, all B applications significantly affected the photosynthetic pigment contents in lavandin, except for the Car content (Tab. 2). Under nonsaline conditions, the high B applications (0.6, 1.2, and 1.8 mM) significantly decreased Chl a content by 27.2%, 38.9%, and 48.7%,

Table 1. Effects of NaCl-salinity and boron on the biomass production of lavandin

Applications (mM)		Fresh weight (g plant^{-1})		Dry weight (g plant^{-1})		Shoot/root ratio	Root length (cm)
NaCl	B	shoot	root	shoot	root		
0	0	13.45 ±0.65 ab	3.78 ±0.35 a	2.96 ±0.20ab	0.349 ±0.04ab	8.48	11.0 ±0.58
	0.3	17.20 ±0.65 a	4.46 ±0.31 a	3.35 ±0.04a	0.418 ±0.02 a	8.01	10.5 ±0.58
	0.6	14.91 ±1.12 bc	4.25 ±0.75 ab	3.43 ±0.18a	0.426 ±0.07 a	8.05	11.2 ±0.44
	1.2	11.70 ±1.92 c	2.72 ±0.61 bc	2.52 ±0.36bc	0.292 ±0.07 bc	8.63	11.3 ±2.73
	1.8	8.10 ±0.78 d	1.68 ±0.31 cd	2.00 ±0.33cd	0.214 ±0.04 cd	9.35	5.8 ±1.83
	means	13.07 A	3.38 A	2.85 A	0.340 A	8.50	10.0 A
80	0	6.92 ±0.40 d	1.08 ±0.10 cd	1.22 ±0.13 e	0.117 ±0.01 d	10.43	7.2 ±1.53
	0.3	6.41 ±0.81 d	1.14 ±0.25 d	1.21 ±0.17 e	0.121 ±0.02 d	10.00	5.4 ±0.49
	0.6	5.95 ±1.22 d	1.25 ±0.58 d	1.16 ±0.28 e	0.117 ±0.04 d	9.91	5.5 ±0.58
	1.2	6.88 ±0.55 d	1.47 ±0.19 d	1.42 ±0.13d e	0.159 ±0.02 d	8.93	5.7 ±0.33
	1.8	5.87 ±0.62 d	1.18 ±0.25 d	1.18 ±0.13 e	0.131 ±0.03 d	9.01	4.5 ±0.01
	means	6.41 B	1.22 B	1.36 B	0.129 B	9,66	5.6 B
F test	NaCl	***	***	***	***		***
	B	***	*	*	ns		*
	NaCl × B	***	*	**	*		ns

Values are the mean of three replicates (means ±SEs, n = 3). Different letters in the same column significantly differ according to the DMRT ($p < 0.05$). *F* test shows a significant difference at: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, and *ns* non-significant

Table 2. Effects of NaCl-salinity and boron on the photosynthetic pigment contents of lavandin

Applications (mM)		Photosynthetic pigment contents (µg g^{-1} FW)				
NaCl	B	Chl *a*	Chl *b*	Chl *a*+*b*	Car	Car/Chl
0	0	712 ±40.6 a	170 ±11.9 a	882 ±52.2 a	417 ±79.9	0.466 ±0.07 e
	0.3	681 ±31.6 a	154 ±7.6 ab	835 ±39.4 a	465 ±22.1	0.557 ±0.01 d
	0.6	518 ±24.0 b	122 ±9.0 bc	641 ±32.5 b	391 ±20.1	0.610 ±0.01 cd
	1.2	435 ±11.3 c	107 ±4.9 c	541 ±13.9 c	377 ±11.1	0.697 ±0.01 b
	1.8	365 ±23.8 d	95 ±4.0 cd	460 ±25.7 cd	347 ±22.2	0.755 ±0.02 ab
	means	542 A	130 A	672 A	399 A	0.617 B
80	0	326 ±20.6 de	114 ±18.8 c	440 ±39.0 de	263 ±22.2	0.597 ±0.03 d
	0.3	295 ±6.8 d	55 ±5.9 e	350 ±12.7 f	239 ±5.4	0.685 ±0.02 bc
	0.6	308 ±18.1 de	11 ±3.5 f	319 ±21.6 f	262 ±5.3	0.728 ±0.03 a
	1.2	282 ±10.4 e	57 ±2.9 e	339 ±13.4 f	251 ±9.7	0.743 ±0.04 ab
	1.8	299 ±13.0 de	69 ±2.6 de	368 ±13.7 ef	281 ±4.8	0.765 ±0.02 ab
	means	302 B	61 B	363 B	259 B	0.704 A
F test	NaCl	***	***	***	***	***
	B	***	***	***	ns	***
	NaCl × B	***	**	***	ns	*

Values are the mean of three replicates (means ±SEs, n = 3). Different letters in the same column significantly differ according to the DMRT ($p < 0.05$). *F* test shows a significant difference at: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, and *ns* non-significant

respectively, compared to the control (B-free). Similarly, the same B applications caused significant decreases in Chl *b* (27.2%, 38.9%, and 48.7%, respectively) and Chl *a* + *b* (27.3%, 38.7%, and 47.8%, respectively). However, all B applications (0.3, 0.6, 1.2, and 1.8 mM) significantly increased the Car/Chl ratio by 19.5%, 30.9%, 49.6%, and 62.0%, respectively, compared to the control (Tab. 2).

Under saline conditions, B application did not significantly affect Chl a content. However, the 0.3, 0.6, 1.2, and 1.8 mM B applications markedly decreased Chl *b* contents by 51.8%, 90.4%, 50.0%, and 39.5%, respectively, compared to the control (B-free). Likewise, the same B applications caused a significant decrease in Chl *a*+*b* content by 20.5%, 27.5%, 23.0%, and 16.4%, respectively. Moreover, the Car content was affected by only NaCl application, and the mean Car content decreased from 399 µg g^{-1} to 259 µg g^{-1}. In contrast to these decreases, the 0.3, 0.6, 1.2, and 1.8 mM B applications significantly increased the Car/Chl ratio by 14.7%, 37.4%, 24.5%, and 28.1%, respectively (Tab. 2).

Concentration, translocation, and accumulation

Under both nonsaline and saline conditions, the concentrations and BCF of B in shoots and roots, the TF of B, and net B accumulation were significantly affected by the application of B (Tab. 3). Under nonsaline conditions, 0.3, 0.6, 1.2, and 1.8 mM B applications caused remarkable increases in the B concentrations in shoots (3.7-, 7.4-, 10.4-, and 13.3-fold, respectively) and roots (1.4-, 1.9-, 4.8-, and 7.3-fold, respectively) compared to the control. Similarly, under saline conditions, all B applications (0.3, 0.6, 1.2, and 1.8 mM) increased the B concentrations in shoots by 2.3-, 3.7-, 7.3-, and 9.1-fold, respectively, compared to the con-

Table 3. Effects of NaCl-salinity and boron on the concentrations, translocation, and net accumulations of boron in lavandin

Applications (mM)		B concentrations (µg g^{-1} DW)		BCF of B		TF of B	Net B accumulation (µg g^{-1} DW)
NaCl	B	shoot	root	shoot	root		
0	0	72.0 ±1.74 g	101.4 ±3.95 e	144.0 ±3.46 a	202.8 ±7.84 b	0.71 ±0.03 e	0.73 ±0.10 e
	0.3	268.5 ±5.33 e	139.7 ±16.0 e	70.7 ±1.38 c	36.8 ±4.21 d	1.98 ±0.25 b	2.44 ±0.18 d
	0.6	530.8 ±6.60 c	194.4 ±3.69de	74.8 ±0.93 c	27.4 ±0.51 de	2.73 ±0.08 a	4.71 ±0.74 c
	1.2	752.3 ±45.0 b	491.8 ±15.6 b	55.7 ±2.63 d	36.5 ±1.67 d	1.54 ±0.12 c	7.24 ±0.44 b
	1.8	960.7 ±42.0 a	744.4 ±55.0 a	47.3 ±2.06 e	36.7 ±5.42 d	1.34 ±0.19 c	9.87 ±0.96 a
	means	516.9 A	334.3	78.5 A	68.1 B	1.66 A	5.00 A
80	0	63.7 ±1.03g	287.5 ±3.45 de	127.3 ±2.09 b	575.0 ±6.93 a	0.22 ±0.01 f	0.97 ±0.13 de
	0.3	145.3 ±1.20f	255.0 ±7.95 e	38.2 ±0.30 f	67.1 ±2.08 c	0.57 ±0.01 e	1.74 ±0.14 de
	0.6	232.7 ±5.87e	260.9 ±26.5 e	32.8 ±0.83 gh	36.7 ±3.73 d	0.91 ±0.08 de	2.13 ±0.35 de
	1.2	463.5 ±10.0d	380.4 ±22.6 bc	34.3 ±0.87 f	28.2 ±1.38 de	1.22 ±0.06 cd	4.68 ±0.55 c
	1.8	579.6 ±7.58c	428.7 ±17.6 b	28.6 ±0.38h	21.1 ±0.87 e	1.36 ±0.04 c	5.95 ±0.72 bc
	means	296.9 B	322.5	52.2 B	145.6 A	0.86 B	3.09 B
F test	NaCl	***	ns	***	***	***	***
	B	***	***	***	***	***	***
	NaCl × B	***	***	***	***	***	**

Values are the mean of three replicates (means ±SEs, n = 3). Different letters in the same column significantly differ according to the DMRT ($p < 0.05$). *F* test shows a significant difference at: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, and *ns* non-significant

trol. Only high B applications (1.2 and 1.8 mM) significantly increased the B concentration in roots by 32.3% and 49.1%, respectively, compared to the control (Tab. 3).

Under nonsaline conditions, all B applications (0.3, 0.6, 1.2, and 1.8 mM) caused significant decreases in the BCF of B in shoots (50.9%, 48.1%, 61.3%, and 67.2%, respectively) and roots (81.9%, 86.5%, 82.0%, and 81.9%, respectively) compared with the control (B-free). Under saline conditions, similar decreases in the BCF of B in shoots and roots were observed with all B applications compared to the control (Tab. 3).

Under nonsaline conditions, the applications of 0.3, 0.6, 1.2, and 1.8 mM B caused significant B TF increases by 2.8-, 3.8-, 2.2-, and 1.9-fold more than in the control group (B-free), respectively. Likewise,

Table 4. Effects of NaCl-salinity and boron on the concentrations of potassium, calcium, and sodium in shoots and roots of lavandin

Application (mM)		K (mg g^{-1} DW)		Ca (mg g^{-1} DW)		Na (mg g^{-1} DW)	
NaCl	B	shoot	root	shoot	root	shoot	root
0	0	35.32 ±0.40b	38.46 ±0.26 a	3.74 ±0.08 d	4.30 ±0.25 b	0.99 ±0.08 d	8.96 ±0.27 d
	0.3	36.84 ±0.41ab	38.05 ±0.24 a	4.54 ±0.05 bc	6.03 ±0.49 a	1.48 ±0.06 d	11.08 ±0.38 d
	0.6	35.37 ±0.96b	35.98 ±0.44 ab	3.78 ±0.15 cd	6.62 ±0.14 a	1.53 ±0.30 d	10.95 ±0.61 d
	1.2	35.10 ±0.73b	33.25 ±1.02 b	3.71 ±0.21 d	4.57 ±0.52 b	1.17 ±0.06 d	7.15 ±0.09 d
	1.8	37.40 ±0.44a	28.16 ±0.61 c	3.69 ±0.11 d	4.90 ±0.33 b	2.34 ±0.03 d	6.78 ±0.28 d
	means	36.01 A	34.78 A	3.89 B	5.29 A	1.50 B	8.98 B
80	0	24.87 ±0.11 e	12.98 ±2.60 de	3.75 ±0.10 d	1.82 ±0.46 e	36.00 ±1.80 b	26.48 ±5.65 c
	0.3	27.43 ±0.50 d	12.95 ±1.30 de	4.91 ±0.49 b	2.16 ±0.14 de	40.12 ±1.52 a	31.26 ±0.62 bc
	0.6	28.10 ±0.15 d	10.53 ±0.14 e	4.45 ±0.21 bcd	2.62 ±0.03 cde	30.54 ±0.96 c	37.28 ±0.47 a
	1.2	27.69 ±0.38 d	12.27 ±0.53 de	4.70 ±0.57 b	2.73 ±0.03 cd	31.88 ±1.63 c	32.93 ±0.07 ab
	1.8	30.28 ±1.05 c	14.26 ±1.67 d	6.24 ±0.13 a	3.35 ±0.04 c	41.60 ±0.16 a	37.95 ±0.48 a
	means	27.67 B	12.60 B	4.81 A	2.54 B	36.03 A	33.18 A
F test	NaCl	***	***	***	***	***	***
	B	***	**	**	***	***	*
	NaCl × B	*	***	**	**	***	*

Values are the mean of three replicates (means ± SEs, n = 3). Different letters in the same column significantly differ according to the DMRT ($p < 0.05$). *F* test shows a significant difference at: *** $p < 0.001$, ** $p < 0.01$, and * $p < 0.05$

the same B applications increased the net B accumulations by 3.3-, 6.5-, 9.9-, and 13.5-fold higher than in the control. Under saline conditions, the applications of 0.3, 0.6, 1.2, and 1.8 mM B caused notable increases in the TF of B (2.6-, 4.1-, 5.5-, and 6.2-fold, respectively) and in the net B accumulations (1.8-, 2.2-, 4.8-, and 6.1-fold, respectively) compared with the control (B-free) – Table 3.

The effects of NaCl and B applications on ion concentrations (K, Ca, and Na) in shoots and roots were significant (Tab. 4). Under nonsaline conditions, compared to the control (B-free), the 1.8 mM B application caused significant increases in the K concentration in shoots by 5.9%, whereas the 1.2 and 1.8 mM B applications caused significant decreases in the K concentrations in roots by 13.5% and 26.8%, respec-

Table 5. Effects of NaCl-salinity and boron on the net accumulations and translocations of potassium, calcium, and sodium in lavandin

Applications (mM)		Net accumulation of cations (mg g^{-1} DW)			TF value of cations		
NaCl	B	K	Ca	Na	K	Ca	Na
0	0	349.7 ±54.3	37.52 ±6.8	17.92 ±2.44	0.92 ±0.02	0.87 ±0.04	0.11 ±0.01 d
	0.3	353.4 ±21.9	44.88 ±3.1	23.76 ±1.08	0.97 ±0.02	0.76 ±0.06	0.13 ±0.01 d
	0.6	337.2 ±49.2	38.51 ±4.1	24.77 ±4.28	0.98 ±0.04	0.57 ±0.01	0.14 ±0.03 d
	1.2	350.5 ±30.8	38.03 ±3.5	17.86 ±1.89	1.06 ±0.05	0.83 ±0.10	0.16 ±0.01 d
	1.8	385.0 ±38.4	39.94 ±2.9	29.24 ±2.82	1.34 ±0.07	0.75 ±0.03	0.35 ±0.02 d
	means	355.2 A	39.78 B	22.71 B	1.05 B	0.76 B	0.18 B
80	0	279.5 ±49.7	41.86 ±7.2	418.9 ±88.8	2.13 ±0.52	2.32 ±0.52	1.53 ±0.39 a
	0.3	293.1 ±21.2	53.20 ±8.8	444.0 ±46.9	2.17 ±0.26	2.29 ±0.26	1.29 ±0.07 ab
	0.6	241.2 ±37.8	38.44 ±4.5	281.8 ±44.3	2.67 ±0.05	1.70 ±0.09	0.82 ±0.03 c
	1.2	268.6 ±30.3	45.77 ±5.1	326.1 ±28.8	2.27 ±0.11	1.72 ±0.19	0.97 ±0.05 bc
	1.8	305.4 ±49.4	62.56 ±6.6	434.3 ±50.3	2.18 ±0.26	1.87 ±0.03	1.09 ±0.01 bc
	means	277.6 B	48.37A	381.0 A	2.28 A	1.98 A	1.14 A
F test	NaCl	*	*	***	***	***	***
	B	ns	ns	ns	ns	ns	ns
	NaCl × B	ns	ns	ns	ns	ns	*

Values are the mean of three replicates (means ±SEs, n = 3). Different letters in the same column significantly differ according to the DMRT ($p < 0.05$). *F* test shows a significant difference at: *** $p < 0.001$, ** $p < 0.01$, and * $p < 0.05$

tively. Moreover, the 0.3 mM B concentration caused a notable increase in the Ca concentration in shoots by 21.4%, while the 0.3 and 0.6 mM B applications caused a notable increase in roots by 40.2% and 54.0%, respectively, compared to the control. The effect of B application on Na concentrations in shoots and roots was insignificant. It was also observed that Na ions mainly accumulated in roots, and the mean Na concentration in roots was 6-fold higher than that in shoots (Tab. 4).

Under saline conditions, all B applications (0.3, 0.6, 1.2, and 1.8 mM) significantly increased the concentrations of K in shoots by 10.3%, 13.0%, 11.3%, and 21.8%, respectively, compared to the control (B-free) – Table 4. The same B applications caused significant increases in the Ca concentrations in shoots at 30.9%, 18.7%, 25.3%, and 66.4%, respectively. The differences were observed in the effects of B applications on the Na concentrations in shoots, and the 0.3 and 1.8 mM B applications caused a notable increase in the Na concentrations in shoots by 11.4% and 15.6%, respectively. However, the 0.6 and 1.2 mM B applications caused notable decreases in this parameter by 15.2% and 11.4%, respectively, compared to the control (Tab. 4).

Under saline conditions, while the K concentrations in the roots were not significantly affected by any of the B treatments, the Ca concentrations in the roots were significantly increased with 0.8, 1.2, and 1.8 mM B applications by 44.0%, 50.0%, and 84.1%, respectively. The same B treatments caused significant increases in Na concentrations in the roots by 40.8%, 24.4%, and 43.3%, respectively, compared to the control.

Table 6. Effects of NaCl-salinity and boron on K/Na, Ca/Na, and Ca/B ratios in shoots and roots of lavandin

Applications (mM)		K/Na		Ca/Na		Ca/B	
NaCl	B	shoot	root	shoot	root	shoot	root
0	0	36.32 ±3.14 a	4.30 ±0.12 ab	3.83 ±0.25 a	0.48 ±0.04 c	52.06 ±2.31 b	42.60 ±3.10 a
	0.3	24.95 ±0.71 bc	3.44 ±0.12 c	3.07 ±0.09 b	0.55 ±0.06 bc	16.91 ±0.24 d	44.70 ±7.06 a
	0.6	24.77 ±4.43 c	3.31 ±0.22 c	2.68 ±0.55 b	0.61 ±0.02 b	7.12 ±0.13 ef	34.11 ±1.26 b
	1.2	30.33 ±2.24b	4.65 ±0.13 a	3.20 ±0.26 b	0.64 ±0.0 7ab	4.94 ±0.08 f	9.25 ±0.79 c
	1.8	15.99 ±0.39 d	4.18 ±0.34 b	1.58 ±0.06 c	0.72 ±0.04 a	3.84 ±2.45 f	6.96 ±1.40 c
	means	26.47 A	3.98 A	2.87 A	0.60 A	16.97 B	27.52 B
80	0	0.69 ±0.03 e	0.49 ±0.02 e	0.11 ±0.01 d	0.07 ±0.01 e	58.93 ±2.45 a	6.35 ±1.69 c
	0.3	0.69 ±0.04 e	0.42 ±0.05 e	0.12 ±0.01 d	0.07 ±0.01 e	33.77 ±3.16 c	8.49 ±0.60 c
	0.6	0.92 ±0.03 e	0.28 ±0.01 e	0.15 ±0.01 d	0.07 ±0.01 e	19.15 ±0.98 d	10.24 ±0.94 c
	1.2	0.87 ±0.04 e	0.37 ±0.02 e	0.15 ±0.01 d	0.08 ±0.01 e	10.16 ±1.17 e	7.24 ±0.49 c
	1.8	0.73 ±0.03 e	0.38 ±0.05 e	0.15 ±0.01 d	0.09 ±0.01 e	10.77 ±0.30 e	7.84 ±0.39 c
	means	0.78 B	0.39 B	0.14 B	0.08 B	26.56 A	8.03 B
F test	NaCl	***	***	***	***	***	***
	B	***	***	***	*	***	***
	NaCl × B	***	**	***	*	**	***

Values are the mean of three replicates (means ±SEs, n = 3). Different letters in the same column significantly differ according to the DMRT ($p < 0.05$). *F* test shows a significant difference at: *** $p < 0.001$, ** $p < 0.01$, and * $p < 0.05$.

The interaction between NaCl and B applications on the net accumulations and translocations (TF) of K, Ca, and Na ions was insignificant except for the TF of Na (Tab. 5). Under saline conditions, the TF of Na significantly decreased with 0.6, 1.2, and 1.8 mM B applications by 44.6%, 36.6%, and 28.8%, respectively. In addition, mean net K accumulations decreased by 21.8% (from 355.2 g g–1 DW to 277.6 g g–1 DW) compared to the mean net accumulation of K under nonsaline conditions. However, the mean net accumulation of Ca and Na significantly increased by 21.6% (from 39.8 µg g^{-1} DW to 48.4 µg g^{-1} DW) and 17-fold (from 22.7 µg g^{-1} DW to 381.2 µg g^{-1} DW), respectively, compared to the obtained mean TF level of K under nonsaline conditions. Similarly, the TF levels of K and Ca significantly increased by 2.2- and 2.6-fold, respectively, compared to the mean TF levels of these ions under nonsaline conditions (Tab. 5).

The interaction between NaCl and B applications in some ion ratios (K/Na, Ca/Na, and Ca/B) in shoots

and roots was significant (Tab. 6). Under nonsaline conditions, all B applications (0.3, 0.6, 1.2, and 1.8 mM) significantly decreased the K/Na ratio in shoots by 31.3%, 31.8%, 16.5%, and 56.0%, respectively. The same B applications also caused a notable decrease in shoots' Ca/Na ratio by 19.8%, 30.0%, 16.4%, and 58.7%, respectively. Similar decreases in the Ca/B ratio in shoots were observed at 67.5%, 86.3%, 90.5%, and 92.6%, respectively, compared to the control (B-free). Moreover, lower B applications (0.3 and 0.6 mM) significantly decreased the K/Na ratio in roots by 20.0% and 23.0%, respectively. However, high B applications (0.6, 1.2, and 1.8 mM) significantly decreased the Ca/B ratio in roots by 19.9%, 78.3%, and 83.7%, respectively, compared to the control (B-free). Furthermore, the 0.3, 0.6, 1.2, and 1.8 mM B applications caused significant increases in the Ca/Na ratio in roots by 14.6%, 27.1%, 33.3%, and 50.0%, respectively, compared to the control (Tab. 6).

Under saline conditions, the effects of B applications on the K/Na, Ca/Na, and Ca/B ratios of shoots and roots were insignificant, except for the Ca/B ratio in shoots, compared to the control. The Ca/B ratio in shoots significantly decreased with the 0.3, 0.6, 1.2, and 1.8 mM B applications by 42.7%, 67.5%, 82.8%, and 81.7%, respectively, compared with the control (Tab. 6).

DISCUSSION

Although B plays a crucial role in many physiological processes during plant growth, the presence of excess B in the rooting medium causes leaf chlorosis and necrosis, and thus biomass production and photosynthetic pigment content often decrease [Landi et al. 2012, Choudhary et al. 2020]. Our results showed that exceptionally high B applications caused significant decreases in shoot and root growth (Tab. 1) and chlorophyll pigment contents under nonsaline conditions (Tab. 2). Decreases in biomass production in plants exposed to excessive B may be associated with reductions in photosynthetic capacity as a result of the toxic effects of B [Özfidan-Konakçı et al. 2020]. This reduction in photosynthetic capacity may adversely affect the electron transport system and reduce carbon dioxide assimilation in leaves [Tsiantas et al. 2019]. Studying the effect of increasing B applications on *Mentha arvensis* and *Cybopogon flexuous* plants, [Choudhary et al. 2020] reported that increasing B applications inhibited shoot and root growth and total chlorophyll and carotenoid contents in the studied plants. Under saline conditions, the B applications significantly decreased the shoot and root growth (Tab. 1) and photosynthetic pigment contents (Tab. 2) compared to the same B levels under nonsaline conditions. These decreases could be explained by the ionic and osmotic stress caused by salinity, especially in roots [Berntein and Kafkafi 2002]. Increases in the shoot/root ratio or decreases in root length under saline conditions indicate that roots are more affected by salinity toxicity than shoots (Table 1). Similar results were reported by Franco et al. [2011b] in purslane plants.

All B applications caused an increase in the B concentrations (in both roots and shoots), net B accumulation, and TF of B under nonsaline and saline conditions. These increases may be attributed to increased B translocation and impaired leaf function (particularly Chl contents) due to B toxicity [García-Sánchez et al. 2020]. In addition, it was observed that B accumulated mainly in the shoots, especially with high B applications (Tab. 3). Generally, B absorbed by the roots from the rooting medium is transported in the xylem sap by transpiration flow and accumulates in the shoots, particularly in the leaves where transpiration flow terminates [Brown and Shelp 1997]. On the other hand, the concentrations or bioconcentrations of B in shoots and the TF of B were observed to be lower under saline conditions than under nonsaline conditions (Tab. 3). It was suggested that B absorption from the rooting medium was affected by various environmental factors resulting from the rooting medium, such as the exchangeable ion amounts and types and the transpiration stream [Brown and Shelp 1997]. Under salinity stress, plants absorb and accumulate chloride (Cl) and Na ions in high concentrations, which can disrupt ion homeostasis [Gupta and Huang 2014]. Yermiyahu et al. [2008] reported that biomass production in plants where B and salinity were applied together was lower than when these stressors were applied individually. Likewise, it was reported that B and salinity stress have an antagonistic effect on wheat [Masood et al. 2012], tomatoes [Carmassi et al. 2013], and purslane [Samet and Çıkılı 2018].

Under nonsaline conditions, high B applications significantly reduced K concentrations in roots compared to shoots (Tab. 4). The decreases in the K concentrations

in roots under B toxicity could be associated with membrane damage, which results in K ion leakage into the apoplast [Özfidan-Konakçı et al. 2020]. Furthermore, the Ca concentrations in the shoots and roots of lavandin significantly increased by only low-B applications under nonsaline conditions. It can be explained by several standard features of B and Ca, such as low mobility in plants, high extracytoplasmic concentration compared to the intracytoplasmic concentration, and their functions in the cell membrane [Van Duin et al. 1987]. Salinity led to an extremely high concentration of Na ions and decreased B and Ca concentrations, especially in roots (Tab. 4). In saline conditions, ionic imbalance usually occurs due to uptake competition between Na and K ions. The uptake of K and Ca ions is likely to be inhibited by Na competition [García-Sánchez et al. 2020]. These results are in line with the findings reported by Munns and Tester [2008], who reported that plants exposed to excessive Na ions may exhibit deficiencies in nutritional minerals, mainly Ca and K ions. Similarly, Ketehouli et al. [2019] reported that reducing mineral concentrations under salinity stress might be attributed to the intense competition in the transport system between Na and other ions, such as K and Ca. Additionally, salinity caused an increase in Na ions, whereas it caused a decrease in shoot and root K concentrations (Tab. 4). This decrease could be attributed to the antagonistic effects of K and Na in plants. Mohamed et al. [2016] stated that the increase in Na absorption could inhibit the influx of K transporters. Table 4 shows that increasing B levels have not affected the K concentration in the shoot, as it is not involved in the K uptake pathway [Wang et al. 2013].

The net ion accumulations via roots refer to the ion concentrations in the whole plant. The net accumulation of Ca and Na showed a significant increase with NaCl application (Tab. 5). Under saline conditions, excessive Na accumulation in plant cells causes low water potential and imbalances in ion uptake, reduced leaf expansion, and decreased photosynthetic rates [García-Caparrós et al. 2017]. Since salinity causes cell membrane damage in roots, shoots, or both, membrane-bound Ca ions can replace Na ions, resulting in increased remobilization of Ca ions. Negatively charged xylem-mobile B compounds could form fast-moving complexes by binding with positively charged Ca ions, facilitating the accumulation of the latter in the aboveground parts of plants [Wimmer et al. 2003]. As seen in Table 5, the translocations of K, Ca, and Na affected only NaCl applications, and salinity stress significantly increased these ion translocations. It was reported that salinity may slow or restrict the transpiration process, and thus, B uptake and its transport and accumulation may be adversely affected [Eraslan et al. 2007].

Increasing B applications in nonsaline conditions caused a notable decrease in shoots' K/Na, Ca/Na, and Ca/B ratios compared to the control. However, the effects of increasing B applications on these ion ratios were not found to be significant and decreased dramatically compared to the nonsaline conditions (Tab. 6). Plants subjected to salinity stress must manage numerous central processes to maintain an optimal K/Na ratio. The most important one is to increase root K uptake, load K ions to the xylem to translocate the shoots, and enhance cellular K influx while simultaneously restricting detrimental cytosolic K efflux [Assaha et al. 2017]. Moreover, salinity could cause Ca deficiency by disrupting Ca distribution in plants and slowing Ca uptake by disrupting the K/Na balance in the membranes [Mohamed et al. 2016]. Hadi and Karimi [2012] also reported that high Na concentrations in the root zone inhibit K and Ca uptake and transport, resulting in lower K/Na and Ca/Na ratios in salt-stressed plants

CONCLUSIONS

Our findings may explain discrepancies in NaCl-salinity and B toxicity relationships regarding plant growth, ion accumulation, and ion concentration in lavandin. Both stress factors had significant effects on plant growth and ion concentration individually. In plants exposed to salinity and B stress simultaneously, significant decreases in biomass production and photosynthetic capacity were observed compared to the plants treated with B alone. However, the effect of B application on these parameters was not found to be significant. In addition, reductions in B concentration and net B accumulation were observed with high B applications in plants where salinity and B were applied together. All of these results suggest that there is an antagonistic effect between salinity and B stresses. In saline conditions, high B concentrations caused a decrease in B concentration in shoots compared to high B applications in nonsaline conditions. In addition, this study shows that transpiration is effective on B

uptake and accumulation in the shoot, as well as ion concentration and diversity in the root zone.

Recent studies indicate that the salinity content of soils is gradually increasing for various reasons and that, therefore, the fertility of soils is decreasing. Crop losses have been reported to occur due to osmotic and ionic stress caused by salinity in the rooting medium. In addition, more studies examining the interaction of B and salinity are needed. These studies can aid in managing soils affected by excess B and salinity.

SOURCE OF FUNDING

This research received no external funding

REFERENCES

Assaha, D.V., Ueda, A., Saneoka, H., Al-Yahyai, R., Yaish, M. W. (2017). The role of Na^+ and K^+ transporters in salt stress adaptation in glycophytes. Front. Physiol., 8, 509. https://doi.org/10.3389/fphys.2017.00509

Berntein, N., Kafkafi, U. (2002). Root growth under salinity stress. In: Plant roots: The hidden half, Waisel, Y., Eshel, A., Kafkafi, U. (eds.), 3rd ed. Marcel Dekker, New York, NY.

Brown, P.H., Shelp, B.J. (1997). Boron mobility in plants. Plant Soil 193(1), 85–101. https://doi.org/10.1023/A:1004211925160

Burkhard, L.P., Arnot, J.A., Embry, M.R., Farley, K.J., Hoke, R.A., Kitano, M., Leslie, H.A, Lotufo, G.R., Parkerton, T.F., Sappington K.G., Tomy, G.T., Woodburn, K.B. (2012). Comparing laboratory and field measured bioaccumulation end points. Integr. Environ. Assessm. Manag., 8(1), 17–31. https://doi.org/10.1002/ieam.260

Carmassi, G., Romani, M., Diara, C., Massa, D., Maggini, R., Incrocci, L., Pardossi, A. (2013). Response to sodium chloride salinity and excess boron in greenhouse tomato grown in semi-closed substrate culture in a Mediterranean climate. J. Plant Nutr., 36(7), 1025–1042. https://doi.org/10.1080/01904167.2013.766209

Choudhary, S., Zehra, A., Naeem, M., Khan, M., Aftab, T. (2020). Effects of boron toxicity on growth, oxidative damage, antioxidant enzymes and essential oil fingerprinting in Mentha arvensis and Cymbopogon flexuosus. Chem. Biol. Technol. Agric., 7(1), 1–11. https://doi.org/10.1186/s40538-019-0175-y

Cikili, Y., Samet, H., Dursun, S. (2016). Cadmium toxicity and its effects on growth and metal nutrient ion accumulation in Solanaceae plants. J. Agric. Sci., 22(4), 576–587. https://doi.org/10.1501/Tarimbil_0000001416

Cordovilla, M.P., Bueno, M., Aparicio, C., Urrestarazu, M. (2014). Effects of salinity and the interaction between Thymus vulgaris and Lavandula angustifolia on growth, ethylene production and essential oil contents. J. Plant Nutr., 37(6), 875–888. https://doi.org/10.1080/01904167.2013.873462

Eraslan, F., Inal, A., Gunes, A., Alpaslan, M. (2007). Impact of exogenous salicylic acid on the growth, antioxidant activity and physiology of carrot plants subjected to combined salinity and boron toxicity. Sci. Hortic., 113, 120–128. https://doi.org/10.1016/j.scienta.2007.03.012

Farooq, M.A., Saqib, Z.A., Akhtar, J., Bakhat, H.F., Pasala, R.K., Dietz, K.J. (2019). Protective role of silicon (Si) against combined stress of salinity and boron (B) toxicity by improving antioxidant enzymes activity in rice. Silicon, 11(4), 2193–2197. https://doi.org/10.1007/s12633-015-9346-z

Franco, J.A., Bañón, S., Vicente, M.J., Miralles, J., Martínez-Sánchez, J.J. (2011a). Root development in horticultural plants grown under abiotic stress conditions – a review. J. Hortic. Sci. Biotechnol., 86(6), 543–556. https://doi.org/10.1080/14620316.2011.11512802

Franco, J.A., Cros, V., Vicente, M.J., Martínez-Sánchez, J.J. (2011b). Effects of salinity on the germination, growth, and nitrate contents of purslane (*Portulaca oleracea* L.) cultivated under different climatic conditions. J. Hortic. Sci. Biotechnol., 86(1), 1–6. https://doi.org/10.1080/14620316.2011.11512716

García-Caparrós, P., Llanderal, A., Pestana, M., Correia, P.J., Lao, M.T. (2017). *Lavandula multifida* response to salinity: Growth, nutrient uptake, and physiological changes. J. Plant Nutr. Soil Sci., 180(1), 96–104. https://doi.org/10.1002/jpln.201600062

García-Sánchez, F., Simón-Grao, S., Martínez-Nicolás, J.J., Alfosea-Simón, M., Liu, C., Chatzissavvidis, C., Pérez-Pérez, J.G., Cámara-Zapata, J.M. (2020). Multiple stresses occurring with boron toxicity and deficiency in plants. J. Haz. Mat., 397, 122713. https://doi.org/10.1016/j.jhazmat.2020.122713

Gupta, B., Huang, B. (2014). Mechanism of salinity tolerance in plants: physiological, biochemical, and molecular characterization. Intern. J. Gen., 2014. http://dx.doi.org/10.1155/2014/701596

Hadi, M.R., Karimi, N. (2012). The role of calcium in plants' salt tolerance. J. Plant Nutr., 35(13), 2037–2054. https://doi.org/10.1080/01904167.2012.717158

Han, S., Tang, N., Jiang, H.X., Yang, L.T., Li, Y., Chen, L.S. (2009). CO_2 assimilation, photosystem II photochemistry, carbohydrate metabolism and antioxidant system of citrus leaves in response to boron stress. Plant Sci., 176(1), 143–153. https://doi.org/10.1016/ j.plantsci.2008.10.004

Javid, M., Ford, R., Norton, R., Nicolas, M. (2014). Sodium and boron exclusion in two Brassica juncea cultivars exposed to the combined treatments of salinity and boron at moderate alkalinity. Biologia, 69, 1157–1163. https://doi.org/10.2478/s11756-014-0412-6

Ketehouli, T., Idrice Carther, K.F., Noman, M., Wang, F.W., Li, X.W., Li, H.Y. (2019). Adaptation of plants to salt stress: characterization of Na^+ and K^+ transporters and role of CBL gene family in regulating salt stress response. Agronomy, 9(11), 687. https://doi.org/10.3390/agronomy9110687

Landi, M., Margaritopoulou, T., Papadakis, I.E., Araniti, F. (2019). Boron toxicity in higher plants: an update. Planta, 250, 1011–1032. https://doi.org/10.1007/s00425-019-03220-4

Lichtenthaler, H.K. (1987). Chlorophylls and carotenoids: Pigments of photosynthetic biomembranes. Meth. Enzymol., 148, 350–382. https://doi.org/10.1016/0076-6879(87)48036-1

Masood, S., Wimmer, M.A., Witzel, K., Zörb, C., Mühling, K.H. (2012). Interactive effects of high boron and NaCl stresses on subcellular localization of chloride and boron in wheat leaves. J. Agron. Crop Sci., 198(3), 227–235. https://doi.org/10.1111/j.1439-037X.2011.00501.x

Miller, R.O. (1988). High-temperature oxidation: dry ashing. In: Handbook of reference methods for plant analysis, Kaira, Y.P. (ed.). CRC Boca Raton, 53–56.

Mohamed, A.K., Qayyum, M.F., Shahzad, A.N., Gul, M., Wakeel, A. (2016). Interactive effect of boron and salinity on growth, physiological and biochemical attributes of wheat (Triticum aestivum). Intern. J. Agric. Biol., 18, 238–244. https://doi.org/10.17957/IJAB/15.0032

Moradi, L., Ehsanzadeh, P. (2015). Effects of Cd on photosynthesis and growth of safflower (*Carthamus tinctorius* L.) genotypes. Photosynthetica, 53(4), 506–518. https://doi.org/10.1007/s11099-015-0150-1

Munns, R., Tester, M. (2008). Mechanisms of salinity tolerance. Ann. Rev. Plant Biol., 59, 651–681. https://doi.org/10.1146/annurev.arplant.59.032607.092911

Özfidan-Konakçı, C., Yildiztugay, E., Elbasan, F.,Yildiztugay, A., Küçüködük, M. (2020). Assessment of antioxidant system and enzyme/nonenzyme regulation related to ascorbate-glutathione cycle in ferulic acid-treated *Triticum aestivum* L. roots under boron toxicity. Turk. J. Bot., 44(1), 36–46. http://doi:10.3906/bot-1904-23

Pandey, A., Khan, M.K., Hakki, E.E., Gezgin, S., Hamurcu, M. (2019). Combined boron toxicity and salinity stress – An insight into its interaction in plants. Plants, 8(10), 364. https://doi.org/10.3390/plants8100364

Parks, J.L., Edwards, M. (2005). Boron in the environment. Critic. Rev. Environ. Sci. Technol., 35(2), 81–114. https://doi.org/10.1080/10643380590900200

Samet, H., Çıkılı, Y. (2019). Response of purslane (*Portulaca oleracea* L.) to excess boron and salinity: Physiological approach. Russ. J. Plant Physiol., 66, 316–325. https://doi.org/10.1134/S1021443719020110

Tanaka, M., Fujiwara, T. (2008). Physiological roles and transport mechanisms of boron: perspectives from plants. Pflügers Archiv – Europ. J. Physiol., 456(4), 671–677. https://doi.org/10.1007/s00424-007-0370-8

Tsiantas, P.I., Papadakis, I.E., Tsaniklidis, G., Landi, M., Psychoyou, M. (2019). Allocation pattern, nutrient partitioning, sugar metabolism, and pigment composition in hydroponically grown loquat seedlings subjected to increasing boron concentrations. J. Soil Sci. Plant Nutr., 19, 556–564. https://doi.org/10.1007/s42729-019-00054-7

Van Duin, M., Peters, J.A., Kieboom, A.P., Van Bekkum, H. (1987). Synergic coordination of calcium in borate-polyhydroxycarboxylate systems. Carbohydr. Res., 162(1), 65–78. https://doi.org/10.1016/0008-6215(87)80201-X

Wang, Y., Wu, W.H. (2013). Potassium transport and signaling in higher plants. Ann. Rev. Plant Biol., 64, 451–476. https://doi.org/10.1146/annurev-arplant-050312-120153

Wimmer, M.A., Muhling, K.H., Lauchli, A., Brown, P.H., Goldbach, H.E. (2003). The interaction between salinity and boron toxicity affects the subcellular distribution of ions and proteins in wheat leaves. Plant Cell Environ., 26, 1267–1274. https://doi.org/10.1046/j.0016-8025.2003.01051.x

Yermiyahu, U., Ben-Gal, A., Keren, R., Reid, R.J. (2008). Combined effect of salinity and excess boron on plant growth and yield. Plant Soil, 304(1), 73–87. https://doi.org/10.1007/s11104-007-9522-z