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Source-sink foliar boron (^{10}B) mobility modulated by carbohydrate synthesis and confers antioxidative defense in sugar beet (*Beta vulgaris* L.) under water deficit conditions

Md. Shah Newaz Chowdhury [a,b], Britta Pitann [a], Md. Sazzad Hossain [a,c], Karl H. Mühling [a,*]

[a] Institute of Plant Nutrition and Soil Science, Kiel University, Hermann-Rodewald-Str. 2, 24118 Kiel, Germany
[b] Department of Agricultural Botany, Sher-e-Bangla Agricultural University, Dhaka 1207, Bangladesh
[c] Department of Agronomy and Haor Agriculture, Sylhet Agricultural University, Sylhet 3100, Bangladesh

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ABSTRACT

Drought is a global abiotic stressor which affects boron (B) availability due to reduced mobility. This is particularly affecting B-demanding crops such as sugar beet. However, linking B translocation dynamics and drought-mitigating factors is largely unknown. Therefore, we hypothesize that foliar B application facilitates B long-distance transport, triggering, e.g., osmoregulation and the antioxidant defense system. Plants were grown under sufficient (2.5 mg kg^{-1}) and deficient (0.25 mg kg^{-1}) conditions of ^{11}B-boric acid for 28 days after sowing, then 24 days of ample and limited water, with or without foliar ^{10}B-boric acid of 300 mg L^{-1}. In this study, it was observed that foliar-applied ^{10}B translocates from source to sink tissue and increases mobility at sufficient ^{11}B supply under water-deficit conditions. Conversely, B-induced accumulation of sucrose and osmolality (ψs) indicates lower foliar ^{10}B transport failure from source to sink tissue. Further, higher levels of H_2O_2 and MDA under B deficiency and limited water supply cause a reduction of dry matter. However, foliar-applied ^{10}B at sufficient ^{11}B resulted in the upregulation of the antioxidant defense systems, as reflected by enzyme activities, e.g., CAT, and AsA-GSH cycle enzymes. In contrast, it leads to a decrease in SOD activity, indicating the cellular redox balance. Our findings highlight and provide unprecedented insights into understanding the dynamics of B translocation from source to sink using B tracers (^{10}B and ^{11}B), where B status delineates the distribution and mobility of foliar B. This suggests protection against ROS and coordination of carbohydrate metabolism while mitigating antioxidative stress.

1. Introduction

Drought is a prevalent environmental stress factor, especially in arid and semi-arid regions across the world. Climate change intensifies this scenario as rising temperatures and unpredictable patterns of rainfall lead to more frequent and severe drought events. This severe stressor increases the challenges for agriculture worldwide by affecting optimal crop yield and resilience (Chaitanya et al., 2024).

The metalloid boron (B) is a micronutrient necessary for the growth and development of vascular plants (Warington, 1923; Wimmer et al., 2009; 2019). It is a fundamental constituent of the primary cell wall to maintain stability and membrane integrity (Cakmak et al., 1995; Matoh, 1997; Mühling et al., 1998; Brown et al., 2002; Wimmer et al., 2009), promotes sugar translocation, influences the biosynthesis of carbohydrates and metabolomic compounds like antioxidants and polyphenols (Bolaños et al., 2023).

In order to maintain a certain threshold level to fulfill its functions in plants, sufficient uptake from the soil is a prerequisite. In this regard, a soil B concentration of 1.0 mg kg^{-1} is classified as sufficient for plant growth (Pommerrenig et al., 2019), whereas a soil B concentration

Abbreviations: APX, ascorbate peroxidase; B, ^{10}B, ^{11}B, boron; CAT, catalase; d, day; DHAR, dehydroascorbate reductase; GR, glutathione reductase; H_2O_2, hydrogen peroxide; MDA, Malondialdehyde; MDHAR, mono dehydroascorbate reductase; ROS, reactive oxygen species; SOD, superoxide dismutase; ψs, osmolality.

* Corresponding author: Karl H. Mühling, Institute of Plant Nutrition and Soil Science, Kiel University, Hermann-Rodewald-Str. 2, 24118 Kiel, Germany.
E-mail addresses: snchowdhury@plantnutrition.uni-kiel.de (Md.S.N. Chowdhury), bpitann@plantnutrition.uni-kiel.de (B. Pitann), shossain@plantnutrition.uni-kiel.de (Md.S. Hossain), khmuehling@plantnutrition.uni-kiel.de (K.H. Mühling).

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below 0.25 mg B kg^{-1} soil characterizes a severe deficiency, a situation that is prominent in >80 countries globally (Shorrocks, 1997). This situation is further intensified by drought. B is further depleted due to reduced mobility and polymerization of boric acid (Barber, 1995; Yoshinari and Takano, 2017), which subsequently alters plant water relations (Wimmer and Eichert, 2013).

Sugar beet *(Beta vulgaris* L.) belongs to the family of Amaranthaceae, including the most B-requiring plants like Brassicaceae (Matoh, 1997; Xue et al., 1998; Wang et al., 2022) and which are potentially prone to a variety of stresses (Hossain et al., 2017a, b; Alavilli et al., 2023). Besides other crops, sugar beet is sensitive to drought, and 5 to 30 % yield loss has been reported (Islam et al., 2020). This is accompanied by reduced sucrose content, and this event is more pronounced in arid areas such as California or southern Europe. However, even in areas generally known for higher rainfall, such as the United Kingdom and parts of Germany, sugar beet production faces increasing challenges due to shifting climatic patterns (Ober and Luterbacher, 2002). In light of climate change, it is anticipated that future drought conditions will also be observed within these regions, thereby impacting the availability of B.

Drought and B-deficient conditions of plants ultimately affect plasma membrane transport, a consequence of plasma membrane disruption due to oxidative stress (Lukaszewski and Blevins, 1996; Zhang et al., 2018; Wang et al., 2023; Chowdhury et al., 2024b). In addition, oxidative stress causes an overaccumulation of ROS in the chloroplast, including H_2O_2 (Cakmak and Römheld, 1997; Begum et al., 2020) and could be measured with stress indicators, e.g., MDA (Cakmak et al., 1995). However, maintaining cellular homeostasis by regulating the balance between ROS generation and effective scavenging is essential for plants to mitigate oxidative stress. To combat elevated ROS under stress, plants have evolved specific antioxidative defense mechanism including superoxide dismutase (SOD; EC 1.15.1.1), ascorbate peroxidase (APX; EC: 1.11.1.11) and catalase (CAT; EC: 1.11.1.6) (Shah et al., 2017), ascorbate and glutathione to combat ROS (Lukaszewski and Blevins, 1996; Cakmak and Römheld, 1997; Chen et al., 2024). Furthermore, osmoprotective solutes such as proline and soluble sugars (e.g., sucrose) are increasingly formed and translocated within the plant (Hossain et al., 2017a).

In contrast to osmoprotectants, B is a phloem immobile element in most plant species. Therefore, to counteract drought-induced B-immobility and reduced soil availability, foliar supply of B may be an appropriate strategy to correct deficiency (Eichert and Goldbach, 2010; Dinh et al., 2021b). But how are B translocation and sugars linked? Previous studies have shown that sucrose significantly affects phloem mobility, uptake, and transport of B by forming B-sucrose complexes (Du et al., 2020). It was reported that the availability of B in leaves and buds increased with foliar B application (Eichert and Goldbach, 2010; Silva et al., 2021). Thus, in accordance with previous studies, foliar application emerges as the optimal fertilization practice when soil B availability is limited (Souza Júnior et al., 2023). Moreover, the phloem also plays a pivotal role in facilitating the movement of foliar B from sink to source leaves in the plant, or from sink to reproductive organs (Huang et al., 2008). The difference between expanded and expanding leaves is related to differential activity in borate influx and efflux channels (Chatzistathis et al., 2021). However, deprivation of B significantly impairs phloem and xylem function and disrupts long-distance B transport (Pommerrenig et al., 2019). So far, most studies have focused on B deficiency in sugar beet based on root B utilization (Song et al., 2021; 2023) and other studies on foliar application (Dordas et al., 2007; Zewail et al., 2020; Wu et al., 2021). However, the mobility of foliar B has been addressed on citrus and cowpea (Du et al., 2020; Silva et al., 2021). Although foliar application is commonly used to overcome B deficiency, limited research has focused on identifying the mobility of foliar B in long-distance transport at B-deficiency and B-sufficient conditions and its role in mitigating oxidative damage in sugar beet under drought stress. Using stable isotope tracers (^{10}B and ^{11}B) is a suitable approach for this investigation. Therefore, we hypothesize that the mobility of foliar B facilitates its long-distance transport under sufficient B conditions and thus modulates osmoregulation and antioxidant defense under drought stress. The main aim of the present study was to elucidate the distribution pattern of B (^{10}B and ^{11}B) and subsequent amelioration mechanisms at different B conditions to mitigate drought stress in sugar beet.

2. Materials and methods

2.1. Experimental setup, growth condition, and treatments

Beta vulgaris cv. Strube salz 3 (Strube Research GmbH & Co. KG, Söllingen, Germany) plants were cultivated in pots with soil substrate at the greenhouse of Institute of Plant Nutrition and Soil Science, Kiel University, Germany at an air temperature of 20 °C/14 °C (day/night); photoperiod of 14/10 h (day/night); relative humidity 65–75%; light intensity 280 µM photon $m^{-2}s^{-1}$ (light meter, Li–198, Lincoln, USA) (Pommerrenig et al., 2022). Both growth conditions B-deficient (0.25 mg $H_3^{11}BO_3$ Kg^{-1} substrate) and B-sufficient (2.5 mg $H_3^{11}BO_3$ Kg^{-1} substrate) (99 % ^{11}B atom abundance, Sigma-Aldrich, USA) were created based on the presence of B in the substrate (<0.1 mg B kg^{-1}substrate). For the experiments, a special type of B-free substrate called 'zero soil substrate' was used, which was a mixture of white peat volcanic clay "Fruhstorfer Nullerde (<0.1 mg B kg^{-1} substrate). The substrate for this experiment was prepared according to Eggert and von Wirén (2017). To prevent heat absorption and evaporation, a white pot with a volume of 6100 ml was used. Each pot contains 3 kg of fresh zero-soil substrate that has undergone a thorough drying and sieving process, with a final size reduction to <2 mm. Basal fertilization consisted of (in g kg^{-1} soil substrate) 0.47 NH_4NO_3, 0.38 KCl, 0.45 K_2SO_4, 0.41 $Ca(H_2PO_4)\bullet H_2O$, 0.56 $MgSO_4\bullet 7H_2O$, 0.019 Fe-EDTA, 0.006 $CuSO_4$ $5H_2O$, 0.011 $ZnSO_4\bullet 7H_2O$, 0.015 $MnSO_4\bullet H_2O$, 0.0006 $(NH_4)_6Mo_7O_{24}\bullet 4H_2O$. Sugar beet seeds were soaked overnight (24 h) in double-deionized water with proper aeration and then sown in Mitscherlich pots containing substrate. Only two healthy seedlings were allowed in each pot after germination. After 28 d of continuous growth at two different B conditions (sufficient vs deficient), plants in the fifth-leaf stage were implemented to the following treatments for 24 days: (1) B-sufficient (+B; 2.5 mg $H_3^{11}BO_3$ kg^{-1} substrate); (2) sufficient-B with foliar 300 mg L^{-1} $H_3^{10}BO_3$ (99 % ^{10}B atom %, Sigma-Aldrich, USA); (3) B-deficient (-B; 0.25 mg $H_3^{11}BO_3$ kg^{-1} substrate); (4) deficient-B with foliar 300 mg L^{-1} $H_3^{10}BO_3$. Furthermore, two water conditions, well-watered (WW; 80 % WHC) and drought stress (DS; 30 % WHC), were tested (Fig. 1). Drought stress was imposed by varying irrigation volumes based on the water holding capacity (WHC) of the substrate, with 30 % WHC referring to severe water stress for sugar beet cultivation (Aksu and Altay, 2020).

The experiment was designed as a completely randomized design (CRD) with four replicates. Followed by Pommerrenig et al. (2019) and prior studies (Supplementary Figs. 3 and 4) optimized concentrations of sufficient, deficient and B foliar treatments (Wu et al., 2021; Souza Júnior et al., 2023) and drought stress (Chołuj et al., 2008; Aksu and Altay,

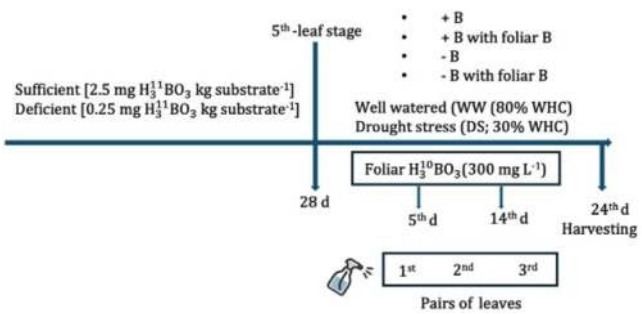


Fig. 1. An illustration showing the experimental setup.

2020) were fixed to enhance the precision of the biochemical investigation. On the 5th and 14th days after implementing drought conditions, foliar application of ^{10}B was carried out on the 1st, 2nd, and 3rd pairs of leaves (Fig. 1). Foliar treatments were conducted in the morning while the greenhouse temperature was low to prevent rapid evaporation of the spray solution. Young leaves and soil were covered with aluminum foil and absorbent paper during foliar spray of ^{10}B ($H_3^{10}BO_3$) to prevent contamination. The solution for foliar spray was prepared by adding Silwet ® Gold (0.1 %), to improve the adhesion to the leaves (Dinh et al., 2021b). Similarly, control plants were sprayed with double deionized water (18.2 MΩ, dH_2O). To confirm ^{10}B mobility and cross-validate soil results, we conduct one more experiment in hydroponic conditions, which allows precise control conditions and minimises soil-related variability with this treatment: control B (+B; 10 μM $H_3^{11}BO_3$) and deficient (-B; 0.25 μM $H_3^{11}BO_3$) treatment conditions for 28 days after transplanting, then 14 days for well-watered (WW) and drought stress (DS) developed by using polyethylene glycol [PEG; molecular weight: 6000, natural, water-soluble, and non-ionic polymer @ 20 %, (w/v)] with foliar 300 mg L^{-1} $H_3^{10}BO_3$ (Supplementary Figs. 4 and 5; see also Supplementary Material). Glassware was not used in any step of the nutrient solution preparation or in the plant watering system to avoid B contamination, e.g., by incorporating B trioxide and double deionized water (18.2 MΩ) was used during conducting the experiments. For precise investigation with repetition, two separate experimental sets with 4 biological replicates were used for measuring growth parameters, including the nutrient status of sugar beet plants, and biochemical investigations. For the accuracy of the data, the whole experiment was repeated twice with four biological replicates, maintaining identical experimental conditions, and each biological replicate was investigated by a minimum of three technical replicates. The entire experiment was conducted based on previous pilot experiments (Supplementary Figs. 2 and 3).

2.2. Growth-related attributes and harvesting

The second true pair of sugar beet leaves was used to measure leaf length (cm) and width (cm) at the final harvest before washing with deionized water using a measuring scale. Mature (treated) and young leaves (untreated), and roots were separated first, and then washed with deionized water. All the samples were oven-dried at 65 °C until constant weight. Dry weights were recorded for shoot and roots, and then samples were ground to fine powder for analysis (Cyclotec 1093, Foss Tecator, Höganäs, Sweden). Fresh shoot samples were collected, immediately frozen in liquid N_2 and stored at −80 °C for biochemical analysis.

2.3. Determination of photosynthetic parameters

A portable chlorophyll meter (SPAD-502, Minolta, Marunouchi, Japan) was used for non-destructive estimation of chlorophyll content. Photosynthetic parameters such as net photosynthetic rate (Pn), stomatal conductance (Gs), transpiration (Tr), and intercellular CO_2 concentration (Ci) were measured in light-adapted plants by using a portable open-flow gas exchange system (LI-6400, LI-COR Biosciences) at photosynthetic photon flux density (PPFD): 1000 μmol $m^{-2}s^{-1}$, LED light source (LI-6400–02, LI-COR Biosciences), flow rate: 500 μmol s^{-1}, CO_2 concentration: 405 μmol mol^{-1} regulation of incoming air was done by CO_2 injection and measuring cuvette temperature: 25 °C. The second pair of fully expanded leaves, excluding the midrib, was selected for the measurement (between 8:30 am and 11:0 am).

2.4. Determination of soluble sugars and proline

To determine soluble sugars, oven-dried samples were ground to a fine powder with a ball mill (MM 200, Retsch GmbH, Haan, Germany). The extraction of soluble sugars was carried out in accordance with Dinh et al. (2021b) with slight modifications. Briefly, approximately 20 mg of powdered oven-dried plant material was dissolved in 1.5 mL deionized water and boiled for 5 min. Subsequently, it was mixed thoroughly and then placed in an ice-water bath for cooling for 30 min. Afterward, samples were centrifuged at 17,500 x *g* at 4 °C for 10 min, and the supernatants were collected. For protein precipitation, 200 μL chloroform was added, and samples were again centrifuged at 17,500 x *g* at 4 °C for 5 min. For purification of the supernatant, it was passed over C18 columns (Strata®. 8B-S001-DAK, Phenomex, Torrance, CA, USA). Afterwards, the organic acids, and soluble sugars were determined by isocratic ion chromatography (IC-5000 Capillary Reagent- Free IC System, Thermo Scientific).

For proline determination, 0.25 g of fresh leaf material was homogenized with 10 mL of aqueous sulfosalicylic acid (3 %), according to Yan et al. (2021). A spectrophotometric measurement was taken at 520 nm. Finally, proline content was calculated by using the absorbance values against the standard curve of known proline concentration.

2.5. Osmolality measurement

The osmolality (ψs) of sugar beet plant leaves was measured, following the method described by Sagervanshi et al. (2022) using a cryoscopic osmometer (Gonotec 030 GmbH, Barlin, Germany).

2.6. Elemental analysis

Macro and micronutrients (including ^{10}B and ^{11}B) concentrations were analyzed by inductively coupled plasma mass spectrometry (ICP-MS; Agilent 7700, Agilent Technologies Inc., USA) as described (Dinh et al., 2021a; Chowdhury et al., 2024a); to avoid B contamination, only plasticware was used in all steps. Other elements except N were analyzed using inductively coupled plasma optical emission spectroscopy (ICP-OES, Agilent Technologies 5800 RV, Santa Clara, CA, USA). The Dumas combustion technique was used to quantify the total nitrogen concentration in leaves and roots dry matter; finely powdered samples of approximately 20 mg were then placed into aluminum capsules for analysis using a CNS elemental analyzer (Flash EA 1112 NCS, Thermo Fisher Scientific, Waltham, MA, USA) to determine N.

2.7. Plant physiological indicators

2.7.1. Production level of oxidative stress indicators

The malondialdehyde (MDA) content was determined according to Heath and Packer's (1968) with slight modification by using 20 % TCA and 0.5 % TBA. First, absorbance readings at 532 nm and final absorbance at 600 nm were estimated, and the extinction coefficient 155 $mM^{-1}cm^{-1}$ was used for calculating the concentration in nmol g^{-1} fresh weight. The hydrogen peroxide (H_2O_2) content in leaves was measured using the modified procedure outlined by Velikova et al. (2000). After homogenizing leaf samples (0.2 g) in 1.6 mL of 0.1 % trichloroacetic acid (TCA) for 30 min in an ice bath, the samples were centrifuged for 20 min at 12,000 × *g* at 4 °C. Subsequently, 1 mL of 1 M potassium iodide (SSKI oral solution) and 0.5 mL of 0.1 M potassium phosphate buffer (K-P buffer; pH 7.8) were added to 0.5 mL of supernatant, and the mixture was left in the dark for one hour. Absorbance was measured at 390 nm, and calculation was done by using a standard curve; data were presented in μmol g^{-1} fresh weight.

2.7.2. Quantification of antioxidant enzyme

The protein concentration of the sample was determined according to Bradford (1976). Here, absorbance was measured at 595 nm using bovine serum albumin as the reference.

Catalase (CAT; EC: 1.11.1.6) activity was measured according to Hossain et al. (2017b) with slight modifications. The reaction was initiated by adding 15 mM H_2O_2 with a 50 mM K-P buffer (pH 7.0) mixture and plant extract. Absorbance was taken at 240 nm for up to one

minute and calculation was done by using an extinction coefficient of 39.4 M^{-1} cm^{-1}.

Ascorbate peroxidase (APX; EC: 1.11.1.11) was detected by the decrease in absorbance at 290 nm after the H_2O_2-dependent ascorbate oxidation following the method of Cui et al. (2023). The activity of APX was calculated using the extinction coefficient of 2.8 mM^{-1} cm^{-1} and expressed as μmol H_2O_2 min^{-1} mg^{-1} protein.

The activity of glutathione reductase (GR; EC: 1.6.4.2) was determined using the procedure outlined by Chowdhury et al. (2024b). The absorbance was recorded at 340 nm using an extinction coefficient of 6.2 mM^{-1} cm^{-1}. The activity of GR was expressed as nmol min^{-1} mg^{-1} protein.

The activity of superoxide dismutase (SOD; EC: 1.15.1.1) was estimated spectrophotometrically at 560 nm according to Hossain et al. (2017b) and Hussain et al. (2024).

The activity of dehydroascorbate reductase (DHAR, EC: 1.8.5.1) was measured according to Nakano and Asada (1981) using DHA, K-P buffer, and GSH. The absorbance was measured at 265 nm, with the extinction coefficient of 14 mM^{-1} cm^{-1}.

The activity of monodehydroascorbate reductase (MDHAR, EC: 1.6.5.4) was evaluated following the method of Hasanuzzaman et al. (2011). The absorbance was recorded at 340 nm, and values were calculated using 6.2 mM^{-1} cm^{-1} as the extinction coefficient.

2.8. Statistical analysis

The experimental data were statistically analyzed using a two-way analysis of variance (ANOVA). The analysis was performed using R Studio (version 4.2.2) R Core Team (2022). Means were then compared using Tukey's honestly significant difference (HSD) test, facilitated by the Agricolae package, at a 95 % confidence level ($p \leq 0$ 0.05) to detect statistically significant differences between means. Results were presented as means with standard error (±SE). Graphs and plots were generated using GraphPad Prism 9 (version 9.5.0, GraphPad Software, San Diego, California, USA). In addition, Pearson correlations between response variables were assessed using the "*corrplot*" package in R.

3. Results

3.1. Effect of foliar B application on growth parameters of sugar beet

A deficient plant with insufficient B over 28 days displays significant growth reduction, leaf yellowing, and stem damage, in contrast to sugar beet plants that have sufficient B (Figs. 2 and 3A-D). Fig. 4 shows that drought stress had a negative effect on the growth under deficient conditions of B in sugar beet plants. This effect was mitigated at sufficient B conditions. Sufficient B (+B), alone or combined with foliar B, subsided the adverse effects of drought stress on sugar beet plants by enhancing the biomass of the shoot and root by 53 %, 33 %, 53 %, and 42 %, respectively, compared to deficient B under drought stress (Fig. 4). However, all the treatments were performed similarly except deficient B in well-watered conditions (Figs. 2 and 4). Moreover, findings showed that leaf length and width, shoot, and root dry matter of sugar beet plants increased with the presence of B and with foliar B under both water conditions (Fig. 4).

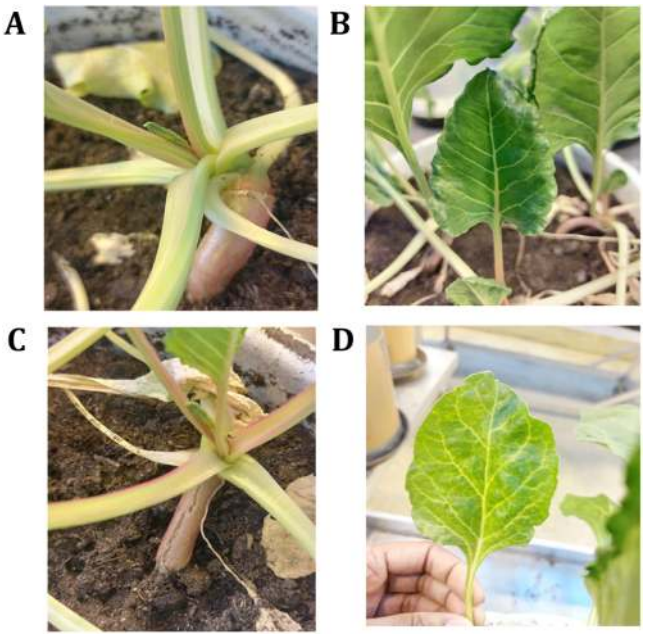


Fig. 3. Phenotypic effects of 2.5 mg ^{11}B-boric acid (kg substrate)$^{-1}$ (A, B) and 0.25 mg ^{11}B-boric acid (kg substrate)$^{-1}$ (C, D) under well-watered conditions on 28-day-old sugar beet plants steam and leaf.

3.2. Effect of foliar B application on B distribution in leaves and roots

The concentration of ^{11}B in mature and young leaves was comparatively higher than in roots under all treatments. Under well-watered conditions, sufficient B (+B) treatment with a foliar ^{10}B application increased ^{11}B concentration compared to deficient B (−B) treatment in sugar beet plants (Fig. 5A–C). Similarly, under drought stress, sufficient B (+B) with additional foliar B application significantly enhanced ^{11}B concentration compared to deficient B (−B) treatment. In mature, young

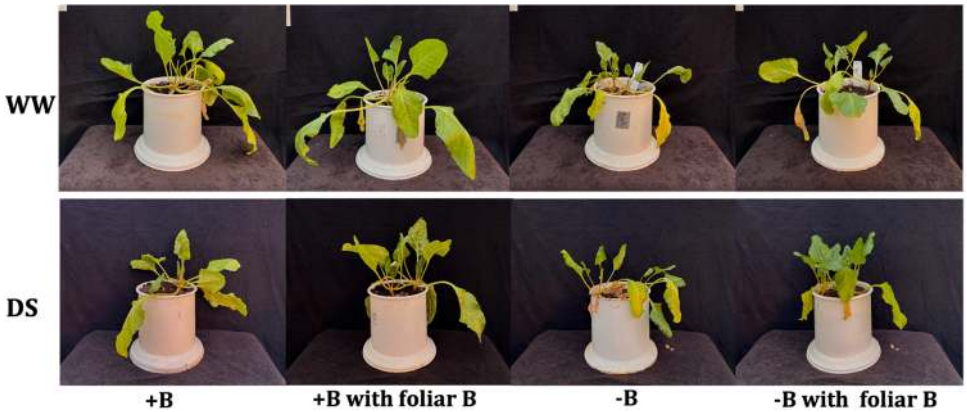


Fig. 2. Provides an overview of the phenotypic effects of foliar B at boron [±] conditions under [WW or DS] on sugar beet. Plants were cultivated under sufficient boron [+B; 2.5 mg ^{11}B-boric acid (kg substrate)$^{-1}$], deficient [-B; 0.25 mg ^{11}B-boric acid (kg substrate)$^{-1}$] treatment conditions for 28 days after sowing, then 24 days for well-watered (WW), and drought stress (DS) with or without foliar 300 mg L^{-1} ^{10}B-boric acid, respectively.

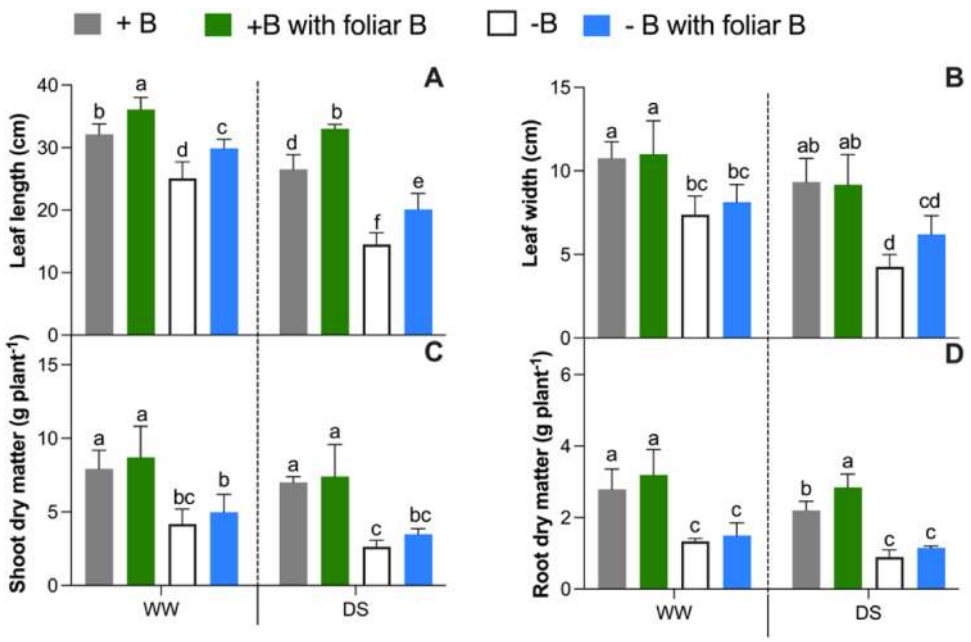


Fig. 4. Effects of foliar boron on growth characteristics A. leaf length (cm), B. leaf width (cm), C. shoot dry matter and D. root dry matter of sugar beet plants. Plants were cultivated under sufficient boron [+B; 2.5 mg ^{11}B-boric acid (kg substrate)$^{-1}$], deficient [-B; 0.25 mg ^{11}B-boric acid (kg substrate)$^{-1}$] treatment conditions for 28 days after sowing, then 24 days for well-watered (WW), and drought stress (DS) with or without foliar 300 mg L^{-1} ^{10}B-boric acid, respectively. The data represent means ± SE (n = 4). Different letters denote significant differences at $p \leq 0.05$ (Tukey's HSD test).

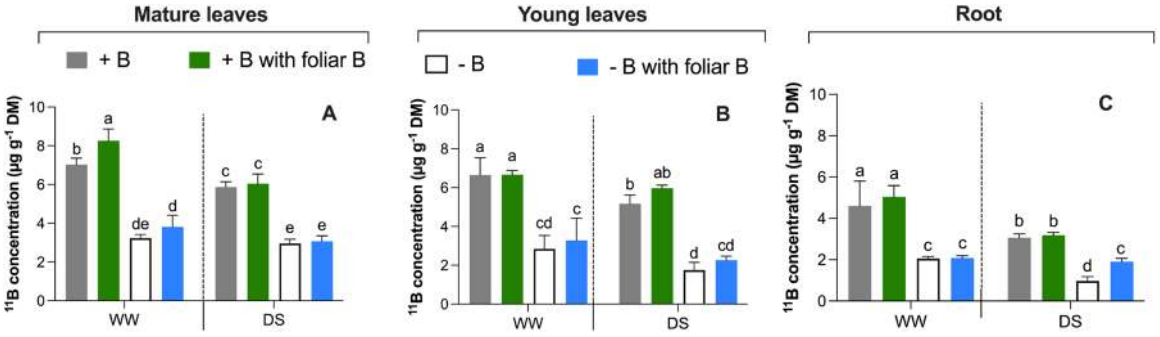


Fig. 5. Effects of foliar ^{10}B-boric acid under drought stress on ^{11}B concentration in A. mature leaves, B. young leaves and C. Roots of sugar beet plants. Plants were cultivated under sufficient boron [+B; 2.5 mg ^{11}B-boric acid (kg substrate)$^{-1}$], deficient [-B; 0.25 mg ^{11}B-boric acid (kg substrate)$^{-1}$] treatment conditions for 28 days after sowing, then 24 days for well-watered (WW), and drought stress (DS) with or without foliar 300 mg L^{-1} ^{10}B-boric acid, respectively. The data represent means ± SE (n = 4). Different letters denote significant differences at $p \leq 0.05$ (Tukey's HSD test).

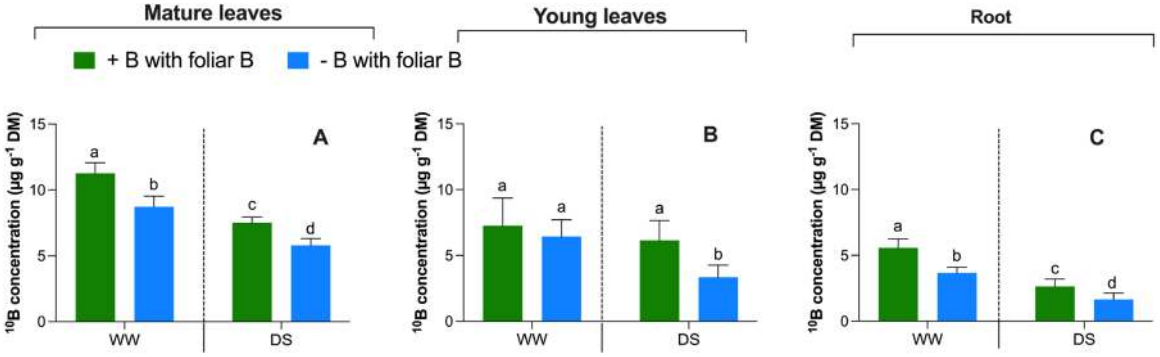


Fig. 6. Effects of foliar boron on ^{10}B concentration in A. mature leaves, B. young leaves and C. Roots of sugar beet plants under drought stress. Plants were cultivated under sufficient boron [+B; 2.5 mg ^{11}B-boric acid (kg substrate)$^{-1}$], deficient [-B; 0.25 mg ^{11}B-boric acid (kg substrate)$^{-1}$] treatment conditions for 28 days after sowing, then 24 days for well-watered (WW), and drought stress (DS) with foliar 300 mg L^{-1} ^{10}B-boric acid, respectively. The data represent means ± SE (n = 4). Different letters denote significant differences at $p \leq 0.05$ (Tukey's HSD test).

leaves and roots, it was 240 %, 97 %, and 228 %, respectively (Fig. 5). In contrast, foliar-applied B at deficient B conditions under drought stress statistically enhances the root ^{11}B concentration compared to B-deficient plants, although unaffected in the leaves (Fig. 5).

Under the same treatments, ^{10}B concentration in mature leaves was higher than in young leaves and roots, as depicted in Fig. 6. Both in leaves and roots, foliar application of ^{10}B increased the concentration of ^{10}B under well-watered and drought stress. Under drought stress, sufficient B (+B) supply, together with foliar B application, increased the ^{10}B concentrations compared to the deficiency of B alone. It was in mature leaves (30 %), young leaves (83 %), and roots (60 %), respectively (Fig. 6).

3.3. Effect of foliar B application on photosynthetic system of sugar beet

Photosynthetic measurements revealed significant differences between deficient and sufficient B (+B) conditions when plants were addressed to foliar B application under well-watered and drought stress (Fig. 7). Results of Pn, Gs, Ci, Tr, and chlorophyll (SPAD values) under drought stress conditions indicated a significant 2.3-, 1.3-, 1.4-, and 2.2-, 1.7-fold reduction when comparing the B-deficient and B-sufficient conditions with foliar B application (Fig. 7). B-deficient (-B) plants independent of foliar B application also significantly differ for all the photosynthetic parameters except Ci at drought stress and Tr at well-watered conditions (Fig. 7D and E).

3.4. Effect of foliar B application on soluble sugar concentration

Soluble sugars, mainly concentrations of sucrose, were higher in mature leaves and roots (Fig. 8). At both water conditions with a deficiency of B (−B), a decline in sucrose concentration was observed in roots compared to sufficient B (+B) supplied plants (Fig. 8I). On the other hand, glucose and fructose concentrations were increased (Fig. 8C and F). In addition, sufficient B, together with foliar application, augmented sucrose concentrations under drought compared to deficiency of B (-B) (Fig. 8). In well-watered conditions with sufficient B (+B) treatment, soluble sugar concentrations in both leaves and roots remained unchanged after foliar B application, except for glucose in young leaves and sucrose concentration in roots (Fig. 8A and I). Overall, deficiency of B led to a decrease in the concentrations of sucrose and the decline was more pronounced under drought (Fig. 8).

3.5. Effect of foliar B application on MDA, H_2O_2, proline content and osmolality

MDA content showed notable differences under varying B conditions (sufficient or deficient) and water regimes (well-water or drought stress) (Fig. 9). Drought-stressed plants had significantly higher MDA levels compared to well-watered plants, particularly under B deficiency (-B) (Fig. 9A). When comparing the effects of foliar B under B-sufficient and B-deficient conditions. Sufficient B (+B) supply showed decreased MDA content compared to deficient B (-B) supply. Remarkably, foliar B application led to a significant reduction of MDA levels by 58 %, 30 %, and 32 %, respectively, under drought stress conditions (Fig. 9A).

Drought stress led to markedly elevated H_2O_2 contents compared to the well-watered system (Fig. 8B). When subjected to drought stress and B deficiency (-B), foliar B significantly reduced the production of H_2O_2 content. Based on the results, compared to sufficient B alone and together with foliar-applied B declined by 13 % H_2O_2 production. In contrast, compared to deficiency of B, sufficient B (+B) together with foliar spray reduced the production of H_2O. It was under drought stress and well-watered conditions by 62 % and 80 %, respectively (Fig. 9B).

Osmolality in sugar beet leaves was significantly different between water levels. However, the foliar B treatments had significant effects (Fig. 9C). The osmolality in leaves of B-sufficient plants with foliar B increased by 48 %, respectively, compared to B-deficient plants without foliar B under well-watered conditions. B-deficient plants under drought stress and without foliar B addition had 82 % lower osmolality compared to B-sufficient plants with foliar B (Fig. 9C).

The findings here revealed that adding B via foliar substantially boosted leaves' proline content under both water systems when B was deficient (-B) in the substrate (Fig. 9D). Based on the results, under drought stress, foliar B application in B-deficient plants resulted in a 116 % accumulation of proline in leaves compared to sufficient B (+B) treatments. On the other hand, sufficient B (+B), individually or combined with foliar B showed a non-significant effect on both water systems (Fig. 9D).

3.6. Foliar B (^{10}B) accelerates the antioxidant properties of sugar beet

3.6.1. APX, CAT, GR, and SOD activities

The activity of APX in well-watered and drought-stressed plants under sufficient B (+B) conditions together with foliar B application was considerably higher compared to those deficient in B (-B) (Fig. 10A). In

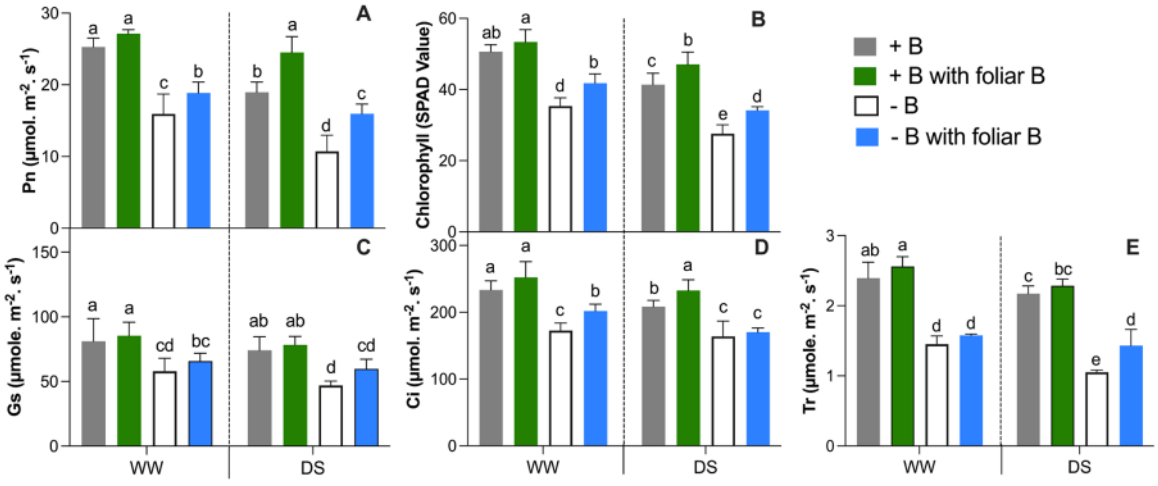


Fig. 7. Influence of foliar boron on photosynthetic performance A. net photosynthetic rate (Pn), B. SPAD value, C. stomatal conductance (Gs), D. intercellular CO_2 (Ci), and E. net transpiration rates (Tr) of sugar beet under drought stress. Plants were cultivated under sufficient boron [+B; 2.5 mg ^{11}B-boric acid (kg substrate)$^{-1}$], deficient [-B; 0.25 mg ^{11}B-boric acid (kg substrate)$^{-1}$] treatment conditions for 28 days after sowing, then 24 days for well-watered (WW), and drought stress (DS) with or without foliar 300 mg L^{-1} ^{10}B-boric acid, respectively. The data represent means ± SE (n = 4). Different letters denote significant differences at $p \leq 0.05$ (Tukey's HSD test).

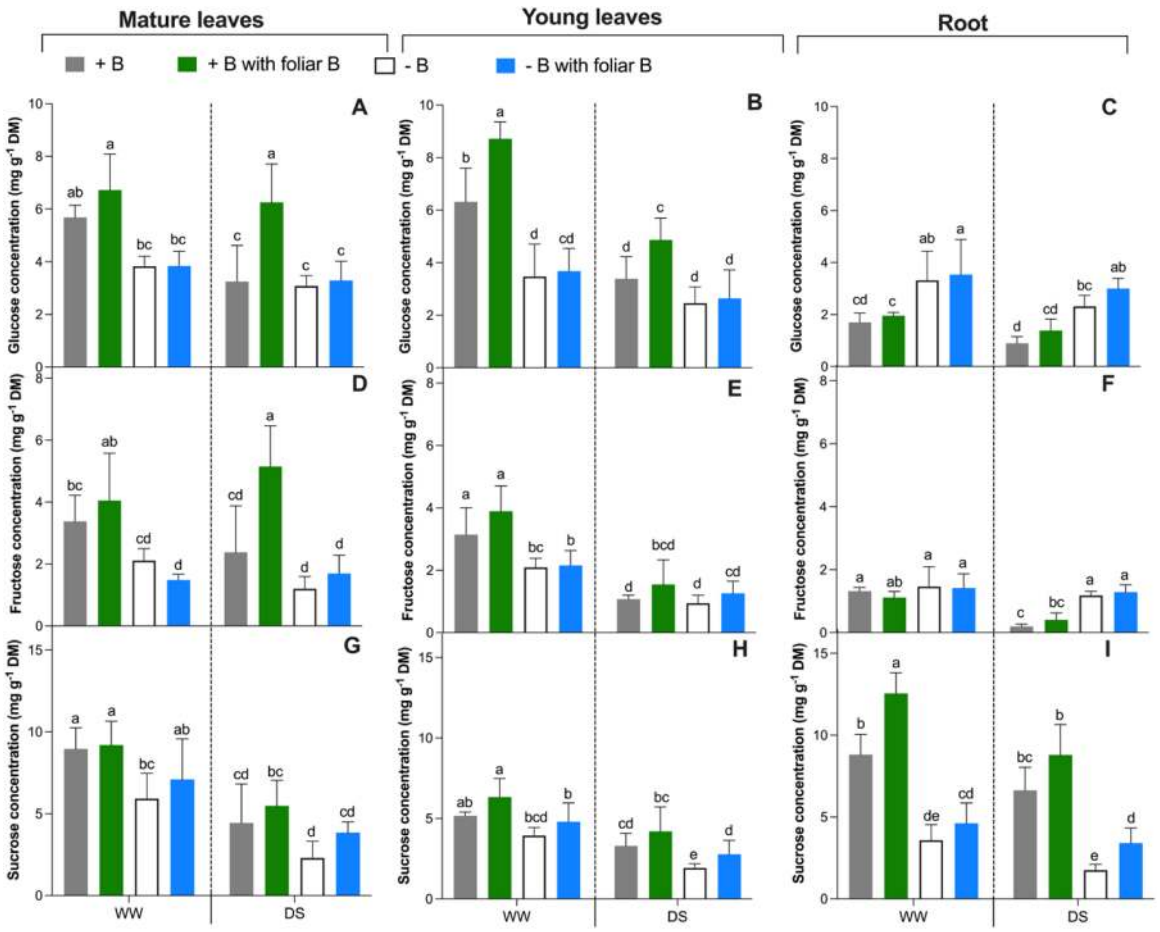


Fig. 8. Influence of foliar boron on glucose (A, B, C), fructose (D, E, F) and sucrose (G, H, I) concentration in mature leaves, young leaves and roots at boron [±] conditions under [WW or DS]. Plants were cultivated under sufficient boron [+B; 2.5 mg ^{11}B-boric acid (kg substrate)-1], deficient [-B; 0.25 mg ^{11}B-boric acid (kg substrate)$^{-1}$] treatment conditions for 28 days after sowing, then 24 days for well-watered (WW), and drought stress (DS) with or without foliar 300 mg L^{-1} ^{10}B-boric acid, respectively. The data represent means ± SE ($n = 4$). Different letters denote significant differences at $p \leq 0.05$ (Tukey's HSD test).

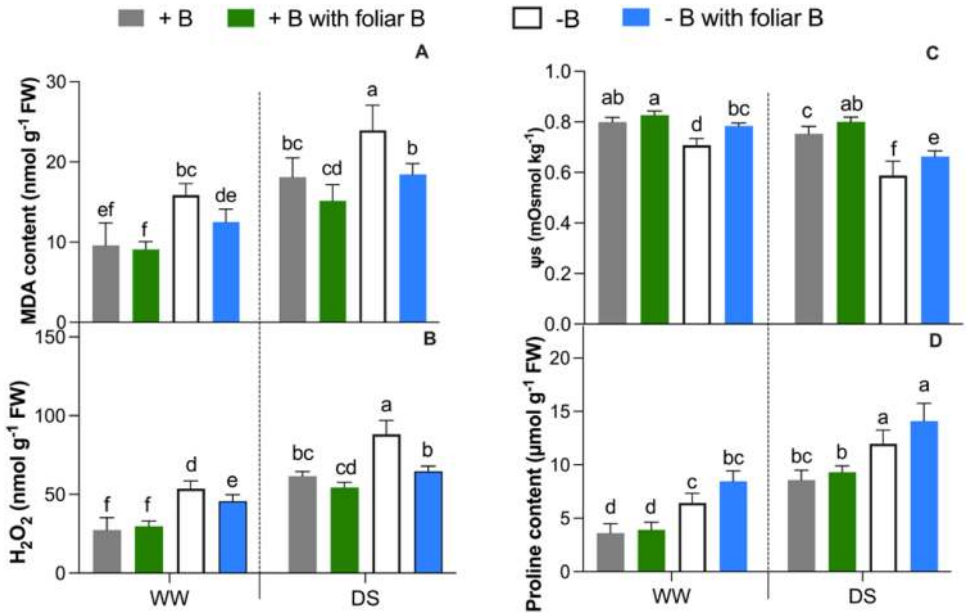


Fig. 9. Influence of foliar boron on the content of A. MDA, B. H_2O_2 C. Osmolality (ψs) D. Proline of sugar beet under drought stress. Plants were cultivated under sufficient boron [+B; 2.5 mg ^{11}B-boric acid (kg substrate)$^{-1}$], deficient [-B; 0.25 mg ^{11}B-boric acid (kg substrate)$^{-1}$] treatment conditions for 28 days after sowing, then 24 days for well-watered (WW), and drought stress (DS) with or without foliar 300 mg L^{-1} ^{10}B-boric acid, respectively. The data represent means ± SE ($n = 4$). Different letters denote significant differences at $p \leq 0.05$ (Tukey's HSD test).

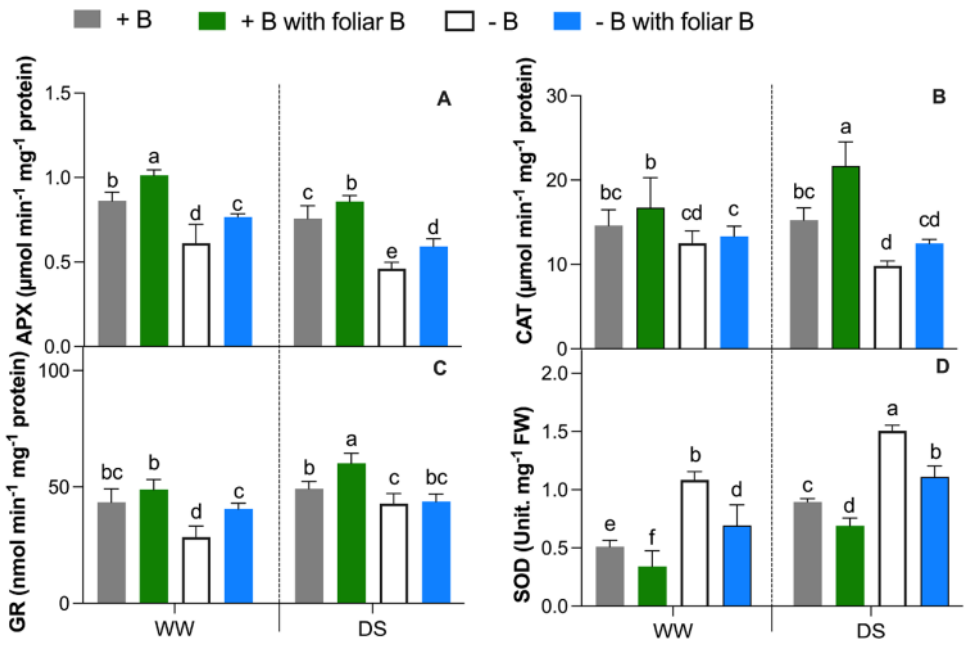


Fig. 10. Effects of foliar boron on A. APX, B. CAT, C. GR, and D. SOD of sugar beet under drought stress. Plants were cultivated under sufficient boron [+B; 2.5 mg ^{11}B-boric acid (kg substrate)$^{-1}$], deficient [-B; 0.25 mg ^{11}B-boric acid (kg substrate)$^{-1}$] treatment conditions for 28 days after sowing, then 24 days for well-watered (WW), and drought stress (DS) with or without foliar 300 mg L^{-1} ^{10}B-boric acid, respectively. The data represent means ± SE (n = 4). Different letters denote significant differences at $p \leq 0.05$ (Tukey's HSD test).

addition, under sufficient B conditions alone, increases of 41 % and 65 % in activities of APX compared to a deficiency of B (Fig. 10A). Overall, sufficient B (+B) alone or combined with foliar B led to accelerated APX activities compared to deficient B conditions (Fig. 10A).

Catalase (CAT) activity in well-watered plants at sufficient B (+B) treatment, with foliar B being enhanced by 34 % compared to deficient B (-B) (Fig. 10B). On the other hand, the combined application showed greater enhancement under drought. It was accelerated by 120 % at sufficient B with foliar compared to deficient B conditions alone (Fig. 10B).

In Fig. 10C, the glutathione reductase (GR) activity increased in both B conditions after foliar spray in drought-stressed plants. When plants were subjected to drought stress, foliar B at sufficient B (+B) conditions increased by 38 % and 40 %, respectively, compared to deficient B with or without foliar B (Fig. 10C). In contrast, no significant differences were observed at sufficient B (+B) under well-watered conditions (Fig. 10C).

It was observed that in Fig. 10D, in both water conditions, the superoxide dismutase (SOD) content in the leaves of deficient B (-B) plants was significantly higher compared to those with sufficient B (+B). Additionally, the effects of foliar B varied significantly in both well-watered and drought-stress conditions. Specifically, SOD levels increased by 39 % under B deficiency in both water conditions (Fig. 10D). When foliar B was applied to plants deficient in B under drought stress, SOD levels decreased by 36 % compared to those without foliar B (Fig. 10D). On the other hand, sufficient B (+B) conditions after foliar B under drought decreased by 61 %, compared to deficient B (-B) with foliar B (Fig. 10D).

3.6.2. *DHAR and mdhar activities*

Dehydroascorbate reductase (DHAR) activity in well-watered plants receiving sufficient B (+B) treatment, with foliar B increased by 60 % in comparison to deficient B (-B) (Fig. 11A). Conversely, the combined application demonstrated a more significant improvement under drought conditions. It was accelerated by 126 % at sufficient B conditions with foliar application compared to the deficient B conditions alone (Fig. 11A).

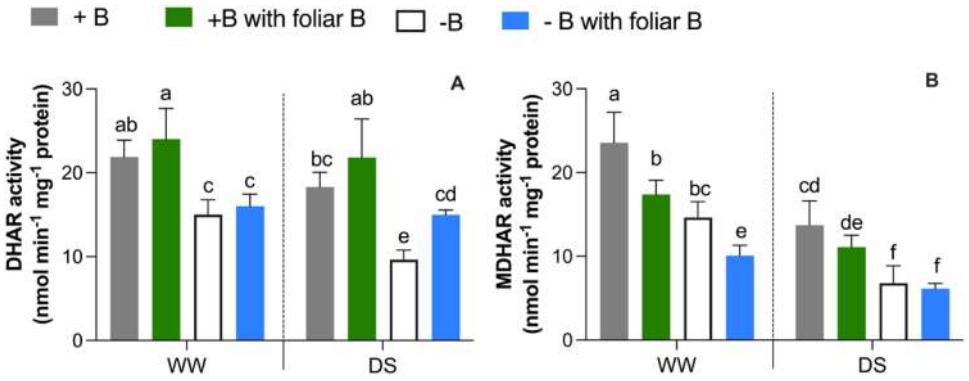


Fig. 11. Effects of foliar boron on A. DHAR, and D. MDHAR activity of sugar beet under drought stress. Plants were cultivated under sufficient boron [+B; 2.5 mg ^{11}B-boric acid (kg substrate)$^{-1}$], deficient [-B; 0.25 mg ^{11}B-boric acid (kg substrate)$^{-1}$] treatment conditions for 28 days after sowing, then 24 days for well-watered (WW), and drought stress (DS) with or without foliar 300 mg L^{-1} ^{10}B-boric acid, respectively. The data represent means ± SE (n = 4). Different letters denote significant differences at $p \leq 0.05$ (Tukey's HSD test).

The activity of monodehydroascorbate reductase (MDHAR) in sugar beet leaves demonstrated significant variations under different B conditions and water regimes. (Fig. 11B). Drought-stressed plants exhibited significantly lowered MDHAR activity compared to well-watered plants, especially under B deficiency (-B) (Fig. 11B). When comparing the effects of foliar B under B-sufficient and B-deficient conditions, sufficient B (+B) supply showed increased leaf MDHAR activity compared to deficient B (-B) supply. Remarkably, foliar B application resulted in a significant increase of MDHAR activity levels by 112 %, 35 %, and 72 %, respectively, under drought stress conditions (Fig. 11B).

3.7. Effect of foliar B application on mineral elements in leaves and roots

The concentrations of macronutrients (N, P, K, Ca, Mg) in leaves significantly differ between water levels; however, the B treatments had significant effects (Fig. 12A–E). The concentrations of N, P, and K in leaves of B-sufficient plants with foliar B were similarly increased, but those of Ca and Mg were 29 % and 48 % higher, respectively, compared to B-deficient plants without foliar under well-watered conditions. B-deficient plants under drought stress and without foliar B addition, shoot concentrations of N, P, K, Ca, and Mg were 52 %, 82 %, 36 %, 90 %, and 91 % lower as compared to B-sufficient plants with foliar B (Fig. 12A–E). The concentrations of micronutrients differ significantly between the well-watered and drought-stress plants. Macronutrients such as Fe, Zn, and Mn concentrations in shoots were 57 %, 34 %, and 58 % higher in the well-watered plants compared to the drought stress in B-sufficient plants with foliar B treatment (Fig. 12F–H). The effect of foliar B nutrition on micronutrient concentrations was nutrient specific: concentrations of Fe, Zn, and Mn were statistically similar to those of B-sufficient plants without foliar at either water condition, but that of B-deficient condition Fe, Zn, and Mn were 39 %, 19, and 42 % lower at without foliar B as compared with B-deficient plants treated with foliar B (Fig. 12F–H). However, B-deficient plants had 120 %, 30 %, and 124 % lower concentrations of Fe, Zn, and Mn in shoots, respectively, as compared to B-sufficient plants with foliar B treatment under drought stress (Fig. 12F–H).

3.8. Pearson correlation

A Pearson correlation analysis was performed (Fig. 13) to find out the general relationships among the response variables at sufficient and deficient B with/without foliar, well-watered, and drought conditions in sugar beet. Dry matters of both shoots and roots showed the highest correlation among them, and a similar pattern was observed for B concentration in mature and young leaves, as well as in sucrose concentration (Fig. 13). Furthermore, photosynthetic parameters show a strong and positive correlation with the concentration of B, sucrose, and the activity of antioxidant enzymes. However, MDA and H_2O_2 strongly and negatively correlated with all parameters. (Fig. 13).

4. Discussions

In sugar beet cultivation, cell division and expansion depend on an abundant water supply, which is closely linked to the uptake of essential plant nutrients (Khan et al., 2023). However, the imposition of drought disrupts water flow dynamics and alters the xylem structure. B is mobilized through the xylem towards the leaves (Miwa and Fujiwara, 2010). In addition, drought increases boric acid polymerization (Barber, 1995). Thus, it affects the translocation and uptake of the B (Yoshinari and Takano, 2017; Pommerrenig et al., 2019). From this perspective, our findings highlight that foliar B positively affects the sucrose concentration in both shoot and root under sufficient B conditions, in contrast to B deficiency (Fig. 14; Supplementary Fig. 6). This probably facilitates the long-distance transport of B, osmotic adaptation and subsequently enhances antioxidant defense during drought.

4.1. Source-sink relations and mobility of B under drought

In the present investigation, 28 days of B deficiency followed by drought conditions significantly reduced growth (Figs. 2 and 3). The

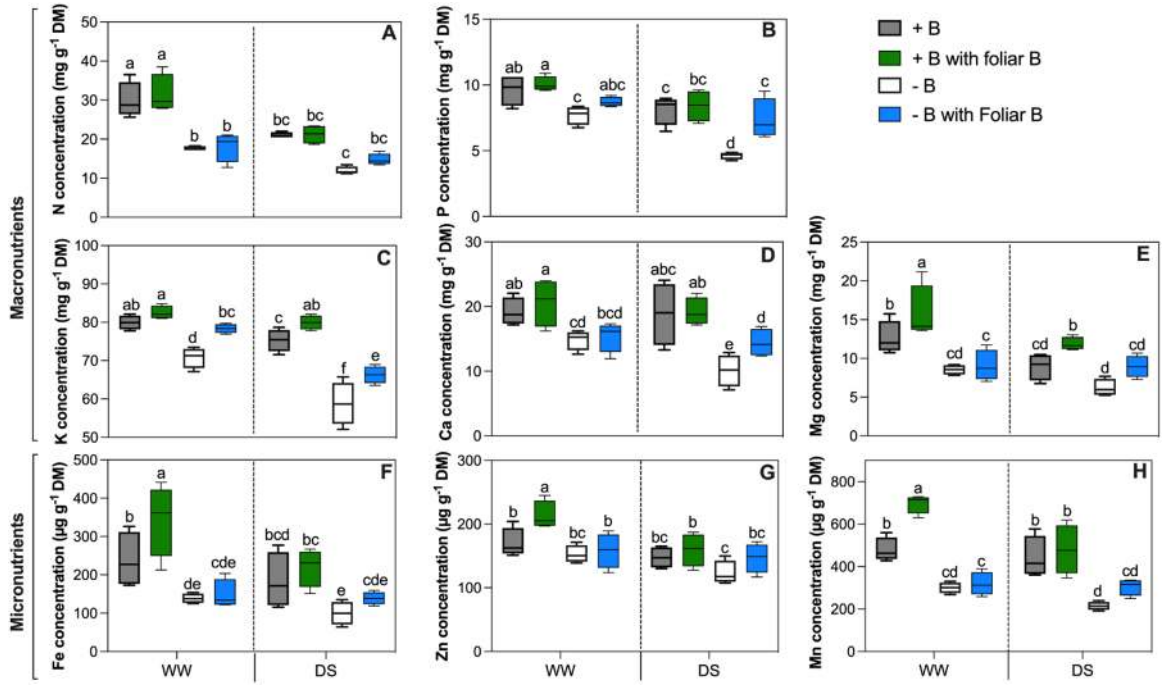


Fig. 12. Overview of the effects of foliar boron (^{10}B) on macro (A-E) and micro (F-H) nutrients concentration of sugar beet under drought stress. Plants were cultivated under sufficient boron [+B; 2.5 mg ^{11}B-boric acid (kg substrate)$^{-1}$], deficient [-B; 0.25 mg ^{11}B-boric acid (kg substrate)$^{-1}$] treatment conditions for 28 days after sowing, then 24 days for well-watered (WW), and drought stress (DS) with or without foliar 300 mg L^{-1} ^{10}B-boric acid, respectively. The data represent means ± SE ($n = 4$). Different letters denote significant differences at $p \leq 0.05$ (Tukey's HSD test).

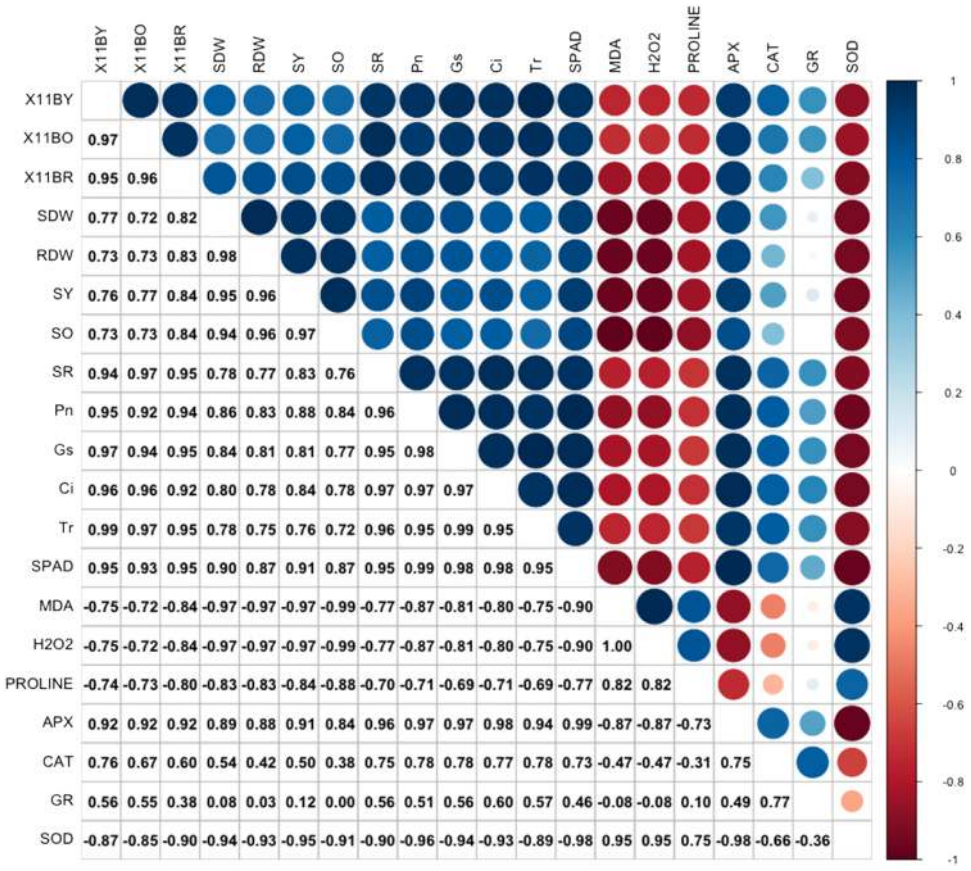


Fig. 13. Correlation analysis of the sugar beet plant's nutrient, growth, osmolytes, physiological, and biochemical characteristics concentration under different treatment conditions. Here, young (X11BY), mature leaves (X11BO), root (X11BR) boron (^{11}B) concentration, shoot and root dry matter (SDW, RDW), sucrose concentration in young (SY), mature leave (SO), root (SR), net photosynthetic rate (Pn), SPAD value, stomatal conductance (Gs), intercellular CO_2 (Ci), and net transpiration rates (Tr), MDA, H_2O_2, PROLINE, APX, CAT, GR, and SOD. The data represent means ± SE (n = 4).

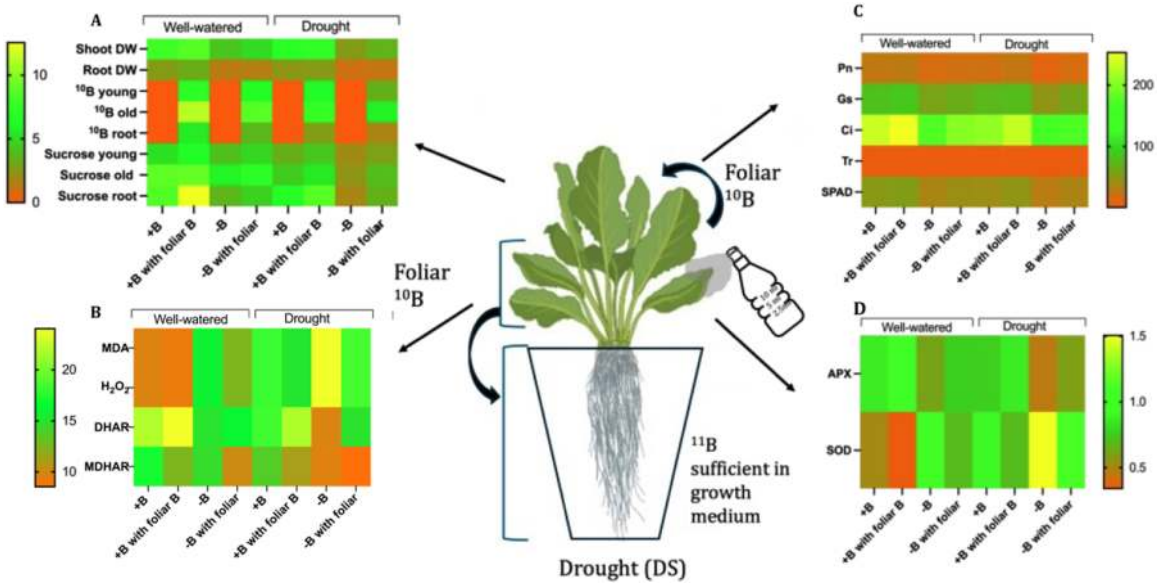


Fig. 14. Schematic illustration of the mobility of foliar boron (^{10}B) on sugar beet and subsiding the destructive effect of drought at boron [±] conditions under [WW or DS] on sugar beet. Plants were cultivated under sufficient boron [+B; 2.5 mg ^{11}B-boric acid (kg substrate)$^{-1}$], deficient [-B; 0.25 mg ^{11}B-boric acid (kg substrate)$^{-1}$] treatment conditions for 28 days after sowing, then 24 days for well-watered (WW), and drought stress (DS) with or without foliar 300 mg L^{-1} ^{10}B-boric acid, respectively.

effects of drought were mitigated by foliar B, particularly under sufficient B conditions (Figs. 2–4). Generally, growth declines under drought conditions owing to constrained water availability. The alteration in plant water relations is manifested through changes in transpiration (Kaur et al., 2021; Lee et al., 2023). Following drought stress, foliar B enhances transpiration (Tr) 2-fold under sufficient B conditions compared to B deficiency (Fig. 7E). Since B transport in the shoot is driven by leaf transpiration, water-limited conditions impede root growth and disrupt the B transport process (Fig. 2, 4 and 13) (Wimmer and Eichert, 2013; Riaz et al., 2019). Simultaneously, the secondary and tertiary effects of B deficiency, illustrated in Fig. 2 and 3, show reduced leaf elongation and stunted growth (Fig. 4A,B).

Despite the immobility of B in many plant species (Whittington, 1957), in this study, foliar B under B-sufficient conditions increased B concentrations in the leaves and roots of both well-watered and drought-stressed plants (Figs. 5 and 6; Supplementary Figs. 2– 4, and 5B). The use of B tracers (^{10}B and ^{11}B) to comprehend B translocation dynamics from source–sink relations provides a unique insight (Matoh and Ochiai, 2005; Will et al., 2012). In this experiment, the foliar application of ^{10}B demonstrated a transport rate of 60 % and 83 % from source leaves to roots and sink leaves, respectively, under conditions of sufficient ^{11}B and drought (Fig. 6C; Supplementary Fig. 5B). According to previous studies, polyols containing castor bean have been found to enhance foliar mobility and root accumulation of B. However, these polyols have also been observed to be affected by transpiration (Eichert and Goldbach, 2010). B-demanding winter oilseed rape showed enhanced benefits from foliar B treatments when applied prior to bud formation (Jankowski et al., 2016). Furthermore, foliar application of ^{10}B has been observed to enhance translocation in young citrus leaves, a process that is further diminished by low root B (Liu et al., 2012). However, root medium concentration gradients have been observed to affect ^{10}B and ^{11}B differently, as reported by Pfeffer et al. (2001) and Dannel et al. (2000). In contrast, in this study, ^{10}B and ^{11}B were applied separately (Fig. 1). It potentially reflected the distribution pattern of ^{10}B and ^{11}B between both leaves after foliar ^{10}B application (Figs. 5 and 6; Supplementary Figs. 3 and 5). Although foliar-applied B did not increase the ^{11}B concentration in young leaves (Fig. 5B), it increased 83 % of ^{10}B concentration under drought stress (Fig. 6B). This implies that sink leaves depend entirely on mature leaves for B during long-term growth under B deprivation (Figs. 13 and 14). Increasing the ^{11}B supply in the root leads to a rise in the ^{10}B concentration in both roots and leaves due to the mobility and redistribution of B within the plant (Canesin et al., 2015). Prolonged B deficiency impairs the translocation of B in the fully extended leaves and roots in tea plants. However, re-translocation occurs in the new leaves of adequately B-supplied plants (Hajiboland and Bastani, 2012). However, long-term B deficiency primarily affects sink tissue, disrupting the normal flow of carbohydrates from source to sink. Consequently, it potentially impairs sink strength (Figs. 2 and 3C). Furthermore, plant physiological responses to drought stress affect the distribution of B from source to sink tissues (Rios et al., 2021).

Notably, sugar beet plants produce polyols and sucrose as the primary photoassimilates. Unfortunately, there is no information on how B carries metabolites and how carbohydrates contribute to the long-distance transport of B under a limited water supply. In addition, B re-translocation occurred in higher polyol-containing species, such as peach, cherry, and apricot, as described by Brown and Shelp (1997). Previous studies reported that B applied to the leaves will be translocated via the phloem by metabolite complexation (Hu et al., 1997; Silva et al., 2021), i.e., the complexation of soluble sugar, e.g., sucrose (Stangoulis et al., 2001; Eichert and Goldbach, 2010; Du et al., 2020). From the results presented here, it can be assumed that foliar-applied B forms complexes with other compounds for long distance transport. Such a crosslink between B and sucrose was also suggested by Du et al. (2020). As demonstrated by Stangoulis et al. (2010) through an in vitro analysis, ^{10}borate or ^{11}borate was found to form a complex with two molecules of sucrose (bis-sucrose borate complex) in phloem exudates of wheat and canola. In addition, Hajiboland et al. (2013) reported that sucrose in tea plants works as a trap to accumulate B and load into the phloem. In poor polyol-producing species, e.g., castor bean (*Ricinus communis*) and elm (*Ulmus glabra*), sucrose acts as a transport metabolite (Lehto et al., 2004; Eichert and Goldbach, 2010). In sugar beet, sucrose is the primary stored and transport sugar (Stanfield and Bartlett, 2022). Higher accumulation enhances resilience against osmotic stress and, thus, vital for the transport form of carbohydrates in the phloem (Chołuj et al., 2008; Hossain et al., 2017a, b). However, an extended period of drought has been shown to curtail available water resources (Hoffmann, 2010) and diminish photosynthesis in sugar beets due to B-deficiency (Song et al., 2021; Wang et al., 2023) (Fig. 7A). In comparison, foliar B under sufficient B conditions increases by 2.3-fold (Fig. 7A), indicating improved drought resilience tolerance. Concurrently, lower sucrose synthesis in the leaves and lower translocation of B was obtained (Figs. 5 and 8). In addition, in B-sufficient conditions, increased sucrose is linked to foliar B's phloem transport to sink leaves and roots (Figs. 6E, 8G, I, and 9C). An increase in B supply raised *SUT4* levels of tobacco, resulting in the elevation of sucrose phosphate synthetase (Shi et al., 2012). In addition, an adequate supply of B in sugarcane enhances the synthesis of carbohydrates and allocation (Martello et al., 2025). In contrast, B deficiency leads to reduced water absorption by altering the expression of aquaporins (Hajiboland et al., 2012). Changes in water accessibility disrupt phloem and xylem transport due to osmotic gradients (Cabrita et al., 2013; White and Ding, 2023). In mature beech trees, damage to the phloem delays sugar export from the leaves under water constraints (Hesse et al., 2019). This breaks down conducting tissues like phloem, restricting sucrose transport from source to sink during drought (Figs. 8H, I, 13, and 14).

However, B forms an ionizable borate-sucrose complex that moves faster across the cellular membrane than the non-ionized sugar molecules (Gauch and Dugger, 1953). Sufficient B condition enhances B mobility in our study (Figs. 6, 8 and 12; Supplementary Fig. 6). Moreover, the phloem's response to drought involves a coordinated interplay between phloem loading and structure to maintain carbon transport (Stanfield and Bartlett, 2022).

4.2. Foliar B mobility accelerates resistance against drought

Proline is a multifunctional amino acid that acts, e.g., as an osmoregulator (Yan et al., 2021) in plants. As a compatible solute regulates anabolic, e.g., protein synthesis and catabolic processes, e.g., osmoregulation in plants under drought, leading to stress resistance (Yan et al., 2021; Chowdhury et al., 2024b). This research observed that a deficiency in B during drought conditions leads to a 116 % increase in proline accumulation (Fig. 9D). Likewise, other studies revealed increased sugar beet tolerance, e.g., drought and salt stress (Alavilli et al., 2023; Tan et al., 2023), and B deficiency (Song et al., 2021). More stress indicators were observed under B-deficient conditions with drought, where a noticeable accumulation of 62 % H_2O_2 was detected in the leaves (Fig. 9B). This observation was confirmed by a 30 % increase in oxidative stress marker malondialdehyde (MDA) (Fig. 9A), which is a by-product of lipid peroxidation. It was observable that both stress markers (MDA and H_2O_2) showed similar trends of correlations in the same treatment level (Figs. 13 and 14A, B). An imbalance of free radicals damages the thylakoid membrane of the leaf, which is reflected by the denaturation of chlorophyll and the photosynthetic system of the stressed plant (Figs. 7A, B, 13, and 14). Recent findings indicate that proline accumulation is directly linked to enhancing tolerance against reactive oxygen species (ROS) (Lu et al., 2023).

The formation of ROS typically occurs in instances of an excess of energy within the chloroplasts that has not been utilized by photosynthesis (Mittler, 2017; Li et al., 2024). As the dynamic balance between ROS generation and scavenging shifts towards generation, plants experience membrane oxidation (Hossain et al., 2017b). Long-time B deficiency causes ROS formation in *Arabidopsis, B. napus, Beta vulgaris*

(Camacho-Cristóbal et al., 2015; Wang et al., 2022, 2023; Song et al., 2023). Therefore, it's reasonable that in the results presented here, sufficient B combined with foliar B under limited water supply enhances leaf assimilation (Pn), intercellular CO_2 (Ci), and stomatal conductance (Gs) (Fig. 7). Reducing CO_2 assimilation rates (Fig. 7A,D) is not solely due to stomatal factors but also non-stomatal factors, indicating a complex interaction affecting photosynthesis (Pn) and overall growth (Figs. 2–4, and 7A). Concurrently, leaf mesophyll carbon dioxide (CO_2) fixation is limited at B-deficient conditions and even with foliar B under drought (Figs. 7C,D, and 13C). B deficiency reduces nicotinamide adenine dinucleotide phosphate (NADPH) activity, thereby affecting redox balance and signaling (Cakmak and Römheld, 1997; Cakmak and Kirkby, 2008), leading to stomatal closure. However, B remarkably reduced H_2O_2 and MDA content (Riaz et al., 2019; Souza Júnior et al., 2023). Therefore, it potentially indicates the growth of sugar beet plants under water-limiting conditions (Fig. 4). Additionally, our results show an increase in osmolality (Fig. 9C). To tolerate and mitigate oxidative stress, SOD activity increases, which mediates a first line of defense for scavenging reactive oxygen species (ROS) (Hossain et al., 2017b; Li et al., 2024). B deficiency and later on water limitation, augmented the activities of SOD, which was decreased by the B supply, indicating a reduction of membrane damage (Figs. 10D and 13). However, over accumulation of ROS under prolonged B deficiency, plants enhance SOD activity as a self-defensive mechanism, thus, indicating the plant under stress (Fig. 10D) (Hossain et al., 2017b; Wang et al., 2023). In contrast, sufficient B with foliar treatment reduces ROS (Fig. 9A,B), which causes a decreasing 61 % SOD activity, indicating relaxation from oxidative stress (Fig. 9D) (Huo et al., 2022). Foliar B decreases SOD activity, which may be due to a shift in the balance of ROS detoxification pathways (Kohnehsharhı and Demir, 2023). In addition, CAT, APX, and GR activities were upregulated in water-limiting-stressed sugar beet plants at sufficient and foliar B conditions (Fig. 10A-C). In addition, the results demonstrated a direct defensive response to H_2O_2, characterized by the modulation of enzyme activities. For instance, the AsA-GSH cycle was found to be intricately linked to the action of several enzymes, including APX, MDHAR, DHAR, and GR (Figs. 9A–D, 10, and 11). (Figs. 11 and 14B). This is crucial in redox balancing because the CAT enzyme acts as a cytosolic H_2O_2 neutralizer (Souza Júnior et al., 2023), while APX plays an important role in mediating the water cycle to dissipate excessive electrons in chloroplast and mitochondria (Cui et al., 2023). However, B deficiency acts as a barrier to enzyme activities, thus likely affecting ascorbate and glutathione synthesis by accumulating ROS (Cakmak and Römheld, 1997). In pea shoots, long-term B starvation reduces the ascorbate and glutathione cycle, key antioxidants essential for redox balance (Chen et al., 2024).

Furthermore, B increases the absorption of N, Ca, K, and Mg (Fig. 12), as reported by Pommerrenig et al. (2018) and Song et al. (2023). Hussain et al. (2024) and Chowdhury et al. (2024b) highlighted that waterlogging and drought stress contribute to the depletion of macronutrients, thereby reducing antioxidative stress defense. Our results also show that essential nutrients like Zn, Fe, and Mn (Fig. 12) increase in the presence of B upon foliar application, contributing to the increased activities of enzymes like CAT and APX, as they are essential co-factors.

In short, by coordinating carbohydrate metabolism and antioxidant defense systems, foliar-applied ^{10}B translocated from source to sink tissues in ^{11}B-sufficient plants and optimized sugar beet growth, indicating the ability of sugar beet to protect against the harmful effects of drought stress.

5. Conclusions

In this study, we designed an approach to an intricate source-sink relationship between B supply and its role in sugar beet's resilience to drought stress, presenting valuable insights into B translocation. The novelty of the present investigation revealed that the B status of the sugar beet plant and the synthesis of photosynthetic assimilated sucrose further influence the mobility of foliar-applied B, as proven by using B (^{10}B, ^{11}B) tracer. This study revealed that foliar-applied B is translocated from source to sink leaves and roots under sufficient B treatment conditions, alleviating drought stress. Overall, it emphasizes how B-sufficient plants enhance osmolytes, sucrose, and is postulated to facilitate foliar B (^{10}B) translocation, and enhance drought stress resistance through augmenting antioxidant enzyme activities (APX, CAT, GR, DHAR, and MDHAR) against ROS.

Declaration

During the preparation of this study, the authors enhanced their English language writing with Grammarly to improve the content's readability. After using this tool, the authors reviewed and edited the content as necessary and take full responsibility for the publication's contents.

CRediT authorship contribution statement

Md. Shah Newaz Chowdhury: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Britta Pitann:** Writing – review & editing, Validation. **Md. Sazzad Hossain:** Writing – review & editing, Validation. **Karl H. Mühling:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.stress.2025.100903.

Data availability

Data will be made available on request.

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