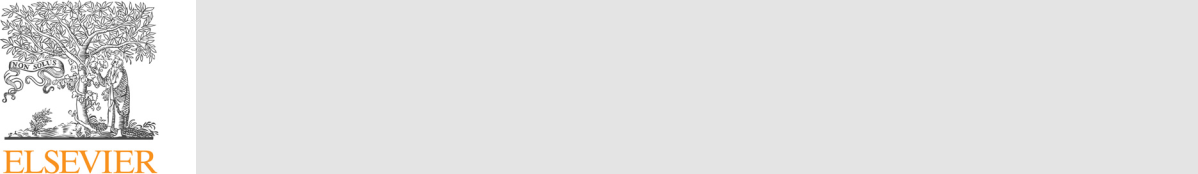
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Multiple stresses occurring with boron toxicity and deficiency in plants

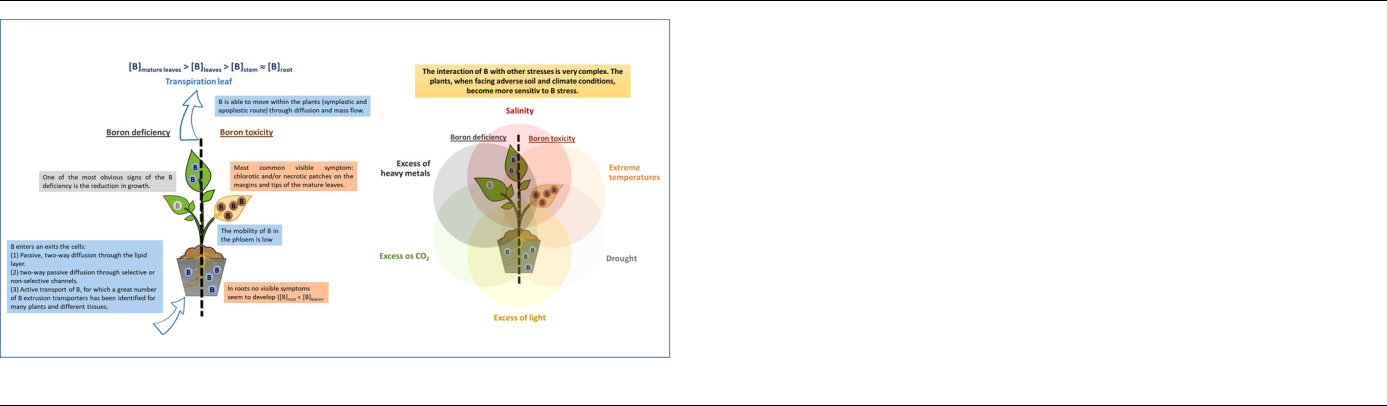
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GRAPHICAL ABSTRACT



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ABSTRACT

Boron (B), an essential nutrient for plants, participates in many physiological processes, with emphasis its role in the formation of the plant’s cell wall. In soil, the range between deficiency and toxicity of B is very narrow as compared to other nutrients, which makes its management in agriculture very diﬃcult, as it depends on the soil and environmental conditions. B stress simultaneously acts with others (extreme temperatures, excess of light, high concentration of CO2, drought, salinity or heavy metal contamination, etc.). The eﬀects of these other stresses could increase the sensitivity of plants to B toxicity or deficiency. The simultaneous combination (B stress × other abiotic stresses) is a complex interaction that should be analyzed in detail if the resistance of crops to climate change is needed. This article reviews the response of plants when facing a combination of B stress with other stresses, and compares this response with the individual stresses. Also, in the last few years, the role of B has been described in multiple plant functions that can improve its resilience to specific stresses. Thus, this article also analyses in what conditions the application of B can be eﬃcient for the improvement of the plant’s response to other stresses.

Abbreviations: ATP, adenosine triphosphate; BOR, selective B transporters; NIP, nodulin 26-like intrinsic proteins; PIP, plasma membrane intrinsic proteins; RG, rhamnogalacturonan; ROS, reactive oxygen species; RWC, relative water content

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1. Introduction

In nature, boron (B) is found as boric acid H3BO3, borate [B(OH)4−], or as borosilicate mineral. B is present in the soil mainly as borosilicate minerals, which contain variable amounts of iron (Fe), aluminium (Al), magnesium (Mg), calcium (Ca), lithium (Li) and sodium (Na). The re-lease of this material in the form of borates is extremely slow, which explains why these minerals cannot supply the quantities of B required by crops that are grown under intense and prolonged cultivation. In most soils, B is found in extremely small quantities, oscillating between 2 and 200 mg kg-1, although most of it is not usable by crops. The factors that aﬀect the amount of B adsorbed by soils and the B bioa-vailability in soils include soil pH, texture, moisture, temperature, and management practices. In the last few years, in arid regions, the use of irrigation water containing high concentrations of B, from various sources such as water from urban and industrial treatment plants, de-salinating plants, waste from surface mining, fly ash industrial chemi-cals, municipal composts, sewage sludge, and eﬄuents from agri-cultural land have resulted in the supply of soil surfaces with highest quantities of B that are excessive for vegetation ([Archana and Verma,](#page7) [2017](#page7)).

B is an essential nutrient for agricultural crops. The quantities re-quired are small, although they vary within certain limits, depending on the plant species, and within species, on the cultivar or variety. The reproductive organs, and to a lesser degree, the leaves, usually contain the highest contents of B. In general, higher contents are found in tubers and legumes, followed by fruit trees and vegetables, with cereals re-quiring the least concentration ([Marschner, 2012](#page7)). Boric acid, is also characterized by its reaction with alcohols, forming B esters. Boric acid, just as borate, can form complexes with a great number of sugars and other compounds that contain cis-hydroxyl groups. This ability to sta-bilize compounds through these complexes is considered the main basis for the understanding of the role of B in biological systems, in-dependently of its function within them.

The main function of B in plants is the maintenance of the structure and the functioning of the cell wall. This element forms rhamnoga-lacturonan-II-B (RG-II-B) complexes that stabilize the pectin network and regulates the size of the cell wall pores. Functions of B in the cy-toskeleton and membrane have also been suggested. However, aside from their structural role in the cells, B also participates in the meta-bolism of nucleic acids and sugars, the synthesis of proteins, phos-phorus metabolism, phenol and nitrogenous compound metabolism and hormonal regulation, among others. These are processes that determine vegetative and reproductive growth (quality of pollen, pollen tube growth), flowering, production and quality of harvest ([Gimeno et al.,](#page7) [2012](#page7)).

At physiological pH, a chargeless form of boric acid exists. The small neutral solutes of this nature have a high permeability through the lipid bilayer of biological membranes. [Yoshinari and Takano (2017)](#page7) have described the three main ways through which B enters and exits the cells: (i) Passive, two-way diﬀusion through the lipid layer, as the bi-layer of phospholipids, the basic structure of the biological membrane, has a high permeability to B; (ii) Two-way passive diﬀusion through selective or non-selective channels. In little more than a decade, a great number of channels or possible channels of B have been identified; (iii) Active transport of B, for which a great number of B extrusion trans-porters has been identified for many plants and diﬀerent tissues. To a certain extent, the most general way in which plants distribute B in their tissues seems to be somewhat uncontrolled when plants are grown in nutrient solutions with a normal range of concentrations of B. In nature, however, plants can be found in B deficient or very B rich soils, so that the plants have to optimize their B absorption and distribution mechanisms to avoid deficiency or toxicity problems, respectively. The solution is to regulate the presence of channels and/or active transport pumps that excrete B.

B is able to move within the plants via the symplastic and apoplastic

route through diﬀusion and mass flow. In the apoplast, the flow of water driven by transpiration can transport any solute that is dissolved in it. Thus, B can very rapidly travel great distances in the xylem. B mobility in the phloem seems to depend on the presence of molecules that are able to form complexes with this nutrient and varies con-siderably among species, although in most plants, the mobility of B in the phloem is low. In sugar alcohol-producing species, such as apple and loquat, borate can bind to sugar alcohols such as mannitol, sorbitol, and dulcitol; the resulting complexes play a role in eﬃcient B re-mobilization from old to young leaves through the phloem ([Oikonomou](#page7) [et al., 2019](#page7); [Tsiantas et al., 2019](#page7); [Papadakis et al., 2018](#page7); [Landi et al.,](#page7) [2019](#page7)). The interaction of the phloem and the xylem in the redistribu-tion of B can be very complex, with the resulting movement of B through every tissue in the plant simply by passive mechanisms being diﬃcult to explain. The membrane transporters could also be im-plicated, aside from the possible existence of an eﬃcient signaling pathway that allows B to mobilize throughout the entire plant ([Mosa](#page7) [et al., 2016](#page7)).

1.1. Boron toxicity

The most common visible symptom in plants exposed to an excess of B is the presence of burns, which appear as chlorotic and/or necrotic patches, often found on the margins and tips of the mature leaves. In roots, as opposed to the leaves, no visible symptoms develop, as the concentration of B is relatively inferior to the roots, even with high concentrations of B in the soil. In species where phloem re-translocation of B occurs, the normal symptoms do not appear. In these cases, dead apical sprouts, abscission of young shoots and lesions in the shape of dry brown patches next to stems and petioles are observed. Among the most-utilized techniques used to avoid B toxicity is the use of grafting ([Simón-Grao et al., 2018](#page7); [Sarafi et al., 2017](#page7)).

The high concentration of B in leaves produces alterations in a great number of physiological processes which include: (i) decreases in the photosynthetic rate and negative eﬀects on the eﬃciency of photo-system II; (ii) increase in lipid peroxidation; iii) alterations of the en-zymes found in antioxidant pathways, (iv) increase in membrane per-meability (v) reduction of the extrusion of protons in the roots, (vi) deposition of suberin and lignin and vii) nutritional imbalances ([Simón](#page7) [et al., 2013](#page7)).

Crops, and even varieties within the same crop, diﬀer in their ability to grow in soils with high concentrations of B. Thus, varieties of wheat (Triticum vulgare Vill.) and barley (Hordeum vulgare) have been identi-fied that were tolerant to an excess of B. In both cases, the tolerant variety had a lower concentration of B in the tissues as compared to those varieties that were considered to be sensitive. In this sense, the basis for B tolerance in those cultivars, which reduce the accumulation of B, can be explained by the high capacity of B eﬄux due to the pre-sence of transporters that remove the B from the cells (BOR) and/or by the decrease of channels of B entry (NIP5 and PIP1) ([Martinez-Cuenca](#page7) [et al., 2015](#page7)). Also, two other mechanisms of tolerance to an excess of B have been described, one of them based on the morphological changes that are produced in the roots, related to the increase in the con-centration of reducing sugars, which allow for the maintenance of the root’s growth; and the other, related to transcription factors. However, in some cases the diﬀerent tolerance among cultivars cannot be ex-plained only by the accumulation of B in the leaves. The studies con-ducted by [Reid and Fitzpatrick (2009)](#page7) in barley and wheat leaves, show that the tolerant varieties have a high expression of Bor2-like genes that are responsible for pumping B from the cytoplasm to the inside of the vacuole where B is less toxic. Thus, a greater quantity of B is accumu-lated without aﬀecting the physiological processes of plants.

1.2. Boron deficiency

One of the most obvious signs of B deficiency is the reduction in

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growth. B deficiency aﬀects very diverse processes such as the growth of the root, the production of indoleacetic acid in the root, the trans-location of sugars, the metabolism of carbohydrates, the synthesis of nucleic acids and the growth of the pollen tube. B deficiency produces changes in the morphology of the root, resulting in an increase in the leaf/root ratio, or a thickening of the root’s cell wall mass due to an accumulation of cellulose, amino acids, phenols and lignin. The end result could be a complete inhibition of the absorption and transport of nutrients. Also, a decrease was found in the levels of antioxidant en-zymes (superoxide dismutase, peroxidase, calatase, and ascorbate per-oxidase), and the values of photosynthetic rate, transpiration rate, stomatal conductance, leaf gas exchange and intercellular CO2 ([Wimmer and Eichert, 2013](#page7)).

B deficiency can also produce damages that have a negative influ-ence on the production and quality of the crops. Thus, in sugar beet, the crown and the heart rot due to the death of the main growing parts of the plant, and the older leaves become brittle and chlorotic. In apples and pears, clear areas of the pulp appear that are full of water, be-coming brown and drying. The surface and the exterior pulp are rough, brownish or reddish, with deep cracks, and the fruit deforms. This can also occur mid-blossom, with the middle flowers withering, becoming black or brown, remaining in the tree for some time. In cherries, piting appears and the fruit flattens, acquiring a wedge shape ([Behboudian](#page7) [et al., 2016](#page7)).

Just as in the case of B toxicity, sensitivity due to B deficiency is a function of the plant’s genotype. Thus, sensitivity to B deficiency is characterized by the loss of ions, accumulation of ROS, lipid perox-idation, plasmolysis, abnormal flower organogenesis and sterility ([Hua](#page7) [et al., 2017](#page7); [Lu et al., 2017](#page7); [Zhou et al., 2017](#page7)).

2. Stress combinations with boron

Climate change is exacerbating the incidence of most of the abiotic stresses on crops. At present, there is a global warming of 1.5 °C over the pre-industrial levels. The global concentration of CO2 has increased in the last few years due to human-caused emissions, from 280 μmol mol−1 to 390 μmol mol−1, and this has been forecasted to increase until reaching values of approximately 550 μmol mol−1 by 2050 ([IPCC, 2014](#page7)). In nature, stress does not generally come in isola-tion and many stresses act synergistically. In response to these stress signals that cross talk with each other, plants have naturally developed diverse mechanisms for combating and tolerating them ([Fig. 1](#page7)).

2.1. Salinity

Salinity is a major abiotic stress for crops, which influences plant growth, development, and yield. Salinity stress has been observed to inhibit plant biomass accumulation, delay plant development, and re-duce photochemical activity in both terrestrial and aquatic plants. There are three main mechanisms of salinity that may aﬀect plants, including the induction of osmotic imbalance, the disruption of ion homeostasis, and the appearance of oxidative stress. Salinity stress can decrease osmotic potential which results in stomatal closure in plants, which will consequently limit water uptake of plants. The ionic im-balance is usually caused by the uptake competition between Na+ and K+. In addition, the uptake of Ca2+ and Mg2+ is also inhibited by Na+ competition, while the oxidative stress in plants is due to the generation of ROS. Also, the ROS induced by salt stress also resulted in lipid per-oxidation ([Syvertsen and Garcia-Sanchez, 2014](#page7)).

In arid or semi-arid areas, excess B and salinity stresses are usually present simultaneously, which may expose plants to the combined stresses of salinity and B toxicity. In previous studies, the combined stresses of salinity and B resulted in more inhibition in the plant than individual salinity or B stress ([Table 1](#page7)). For example, the combination of 10 dS m−1 of salinity and 2.5 mg kg −1 of B had a greater inhibitive eﬀect on plant growth and biomass accumulation of rice than the

individual stresses, partly due to the increase in Na+ and B influxes ([Farooq et al., 2015](#page7)). For salt-sensitive plants, high salinity stress, which is greater that their threshold for tolerance, has been reported to increase the membrane permeability of plants, enhancing B uptake (). Salinity can also aggravate oxidative stress under B toxicity, which may cause more damage to plants ([Eraslan et al., 2007](#page7)). However, salinity stress has also been observed to alleviate B toxicity in some other stu-dies. Thus, the combination of 5 mg L−1 of B and 5 dS m−1 of salinity increased the speed and rate of germination of guayule. Also, the in-hibition of the growth of Puccinellia tenuiflora caused by B was alle-viated by salinity due to B uptake inhibition under B stress. Salinity stress has been reported to reduce transpiration of plants, which re-stricts the uptake and transport of B ([Yermiyahu et al., 2008](#page7)). The use of rootstocks has been shown to increase the number of variables that influence the response of crops to the combination of both types of stress ([Sotiropoulos et al., 2006](#page7); [Grattan et al., 2015](#page7)). Although the combined stresses of B and salinity are complex, it was inferred that salinity could mitigate B toxicity when the concentration of salt was lower than the tolerance threshold of the plant.

There are few studies that have focused on the interactions between salinity and B deficiency. The scarcity of this nutrient can reduce the biomass and relative water content (RWC) of plants, and salinity stress may induce a greater reduction in RWC. Conversely, B deficiency can alleviate the inhibition of biomass increase and the reduction in RWC caused by salinity stress. However, in canola (Brassica napus L.), B de-ficiency has been shown to aggravate the inhibition of plant growth caused by salinity ([Hosaini et al., 2009](#page7)). Salinity stress has also been found to reduce the number of aquaporins of the plant cells to limit B uptake. Moreover, salinity stress has increased the amount of ATPase protein, which could increase the tolerance of plants to B and salinity. The combined eﬀects of salinity and B deficiency are dependent on the B and salinity tolerance threshold of plants. Below this tolerance threshold, the eﬀect of B deficiency and salinity may be antagonistic, and it may become additive when moving beyond this threshold. The interaction between B and salinity is important for the phytoremedia-tion of B-contaminated soil and water ([Karimi and Tavallali, 2017](#page7)).

2.2. Drought

Drought is one of the main factors of abiotic stress that aﬀect the growth of plants all over the world. In crops, among other eﬀects, drought has been shown to decrease stomatal conductance, transpira-tion and photosynthesis, induce the creation of reactive oxygen species and stimulate the activity of enzymatic oxidation ([Zhi et al., 2018](#page7)). Throughout evolution, plants have developed adaptations to water stress. Thus, C4 metabolism and Crassulacean acid metabolism allow plants to explore more arid environments. Other responses include the decrease of leaf expansion and the increase of the root’s growth, the closing of stomata, the synthesis of osmolytes, proteins with protective functions, antioxidant enzymes, transcription factors and other proteins ([Mancosu et al., 2015](#page7)).

Toxicity due to B is frequent in arid and semi-arid regions with subterranean waters with a high content of B or in soils irrigated with water from seawater desalinating plants and urban wastewater treat-ment plants ([Simón-Grao et al., 2018](#page7)). Drought can have an influence on the eﬀects of B toxicity when plants are exposed to both stresses in combination ([Liu et al., 2018](#page7)). Thus, water stress has been demon-strated to reduce the negative eﬀects due to excess B in the irrigation water on the productive output and transpiration of tomato (Solanum lycopersicum L.). Also, reduction in the absorption of B and oxidative stress has also been found when these two stresses were combined in watermelon (Citrullus lanatus). The plants treated with the highest concentration of B, in conditions of water stress, had a greater glu-tathion reductase activity. This was considered to be an important physiological response of watermelon plants as compared to the com-bination of B toxicity and drought. An inhibition of B and Na+

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Table 1

Interaction between B toxicity and deficiency with other stresses. +B: toxicity due to B; -B: B deficiency. In the interaction, “-” means that the negative eﬀect on the growth parameters of the individual factor is less acute than in the combination of stresses; “+” indicates that the negative eﬀect on the growth factors of the individual factor is more acute than in the combination of stresses; Lastly, “ns” means that the eﬀects of some of the growth parameters of the combination of stresses and the stress indicated at the beginning of the column are similar.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Stress Combination | Crop | Interaction B Salt | | | Salt and Boron level | Reference | |
|  |  |  |  |  |  |  |  |
| +B × Salinity | Wheat (Triticum aestivum) | – | – | | Salt: 100 mM NaCl NaCl-B: 100 ppm | [Lata et al., 2017](#page7); [Kumar et al., 2015](#page7) | |
|  | Wheat (Triticum aestivum) | – | – | | Salt: 125 mM NaCl NaCl-B: 6 mM B | [Mohamed et al., 2016](#page7) | |
|  | Wheat (Triticum aestivum) | – | – | | Salt: 100 mM NaCl NaCl-B: 200 μM B | [Wimmer and Goldbach, 2012](#page7) | |
|  | Wheat (Triticum aestivum) | – | – | | Salt: 75 mM NaCl NaCl-B: 200 μM B | [Masood et al., 2012](#page7) | |
|  | Pistachio (Pistacia vera) | – | – | | Salt: 0−3.2 g kg−1 NaCl-B: 0−20 mg kg−1 B | [Karimi and Tavallali, 2017](#page7) | |
|  | Tomato (Solanum lycopersicum) | – | – | | Salt: 40 mM NaCl-B: 0−20 mg kg−1 soil | [Alpaslan and Gunes (2001)](#page7) | |
|  | Cucumber (Cucumis sativus) | – | – | | Salt: 40 mM NaCl-B: 0−20 mg kg−1 soil | [Alpaslan and Gunes (2001)](#page7) | |
|  | Maize (Zea mays) | – | – | | Salt: 15 SAR-B: 0−4 mg kg−1 soil | [Imran et al., 2010](#page7) | |
|  | Broccoli (Brassica oleracea L. var. itálica) | – | – | | Salt: 40 mM NaCl-B: 0−24 ppm | [Smith et al., 2010](#page7) | |
|  | Rice (Oryza sativa) | – | ns | | Salt: 10 dS m−1-B: 2.5 mg kg−1 soil | [Farooq et al., 2015](#page7) | |
|  | Lettuce (Lactuca sativa) | – | ns | | Salt: 12−19 dS m−1-B: 300 μM | [Eraslan et al., 2007](#page7) | |
|  | Pepper (Capsicum annuum) | ns | – | | Salt: 0−45 mM NaCl-B: 0.046−0.740 mM | [Yermiyahu et al., 2008](#page7) | |
|  | Puccinellia tenuiflora | + | ns | | Salt: 0−5 g kg−1 NaCl-B: 0.25−400 mg kg−1 soil | [Liu et al., 2018](#page7) | |
| -B × Salinity | Pistachio (Pistacia vera) | – | – | | Salt: 0−3.2 g kg−1 NaCl-B: 0 mg kg−1 B | [Karimi and Tavallali, 2017](#page7) | |
|  | Canola (Brassica napus L.) | – | – | | Salt: 3−12 dS m−1 NaCl-B: 0 mg kg−1 B | [Hosaini et al., 2009](#page7) | |
|  | Pepper (Capsicum annuum) | – | ns | | Salt: 6 dS m−1 NaCl-B: 0 mg kg−1 B | [Supanjani and Lee, 2006](#page7) | |
|  |  |  |  |  |  |  |  |
| Stress combination | Crop |  | Interaction B Light | | Light and B level | Reference | |

+B × light Cowpea (Vigna unguiculata)

-B × light Cowpea (Vigna unguiculata)

Sunflower (Helianthus annuus)

Black gram (Vigna mungo)

Geranium (Pelargonuim x hortorum L.)

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| – | – | Light: 1900 μmol m−2 | | s-1 | | B: 50 ppm | Inbaraj and Muthuchelian, 2011 |
| – | – | Light: 1900 μmol m−2 | | s-1 | | B: 0 ppm | Inbaraj and Muthuchelian, 2011 |
| – | – | Light: 100 μmol m−2 | s-1 | | B: 0.1 μM | | [Cakmak et al., 1995](#page7) |
| + | ns | Light: 30 % natural light B: 1 μM H3BO3 | | | | | [Noppakoonwong et al., 1993](#page7) |
| – | ns | Light: 100 μmol m−2 | s-1 | | B:0μM | | [Mishra et al., 2009](#page7), [2012](#page7), 2014 |

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Stress combination | Crop | Interaction B CO2 |  |  | CO2 and B level | Reference | |
|  |  |  |  |  |  |  |  |
| +B × CO2 | Barley (Hordeum vulgare) | ns | – |  | High CO2 | [Mishra et al., 2012](#page7) | |
| -B × CO2 | Barley (Hordeum vulgare) | + | – |  | High CO2 | [Mishra et al., 2012](#page7) | |

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Stress combination | Crop | Interaction B Al |  | Al and B level | | Reference | |
|  |  |  |  |  |  |  |  |
| -B × Al | Soybean (Glycine max) | – | ns | Al: 5 mM B: 0 μM | | [Yang et al., 2004](#page7) | |
|  | Soybean (Glycine max) | – | – | Al: 24 μM B: 0 μM | | [Stass et al., 2007](#page7) | |

Although the combined stresses of B and salinity are complex, it was inferred that salinity could mitigate B toxicity when the concentration of salt was lower than the tolerance threshold of the plant.

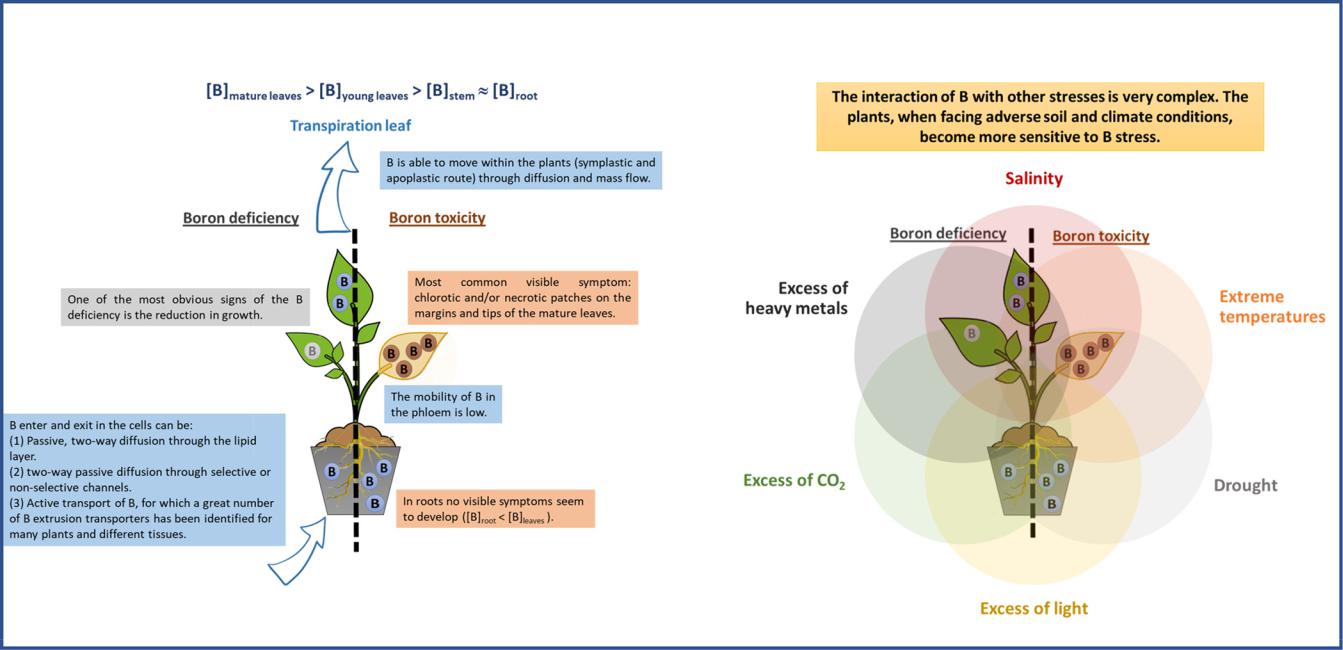


Fig. 1. Distribution of B in plants and its interactions with abiotic stresses.

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absorption and an improvement in the transport of Ca2+ and Mg2+ from the roots to the shoots was also found when both stresses were combined. In a study with wheat (Triticum vulgare Vill.) varieties, one tolerant and another sensitive, to determine their response to B toxicity, it was concluded that the tolerance to both stresses were related, due to the induction and maintenance of a high activity of specific antioxidant enzymes, such as superoxide dismutase, guaiacol peroxidase and as-corbate peroxidase ([Erdal et al., 2014](#page7)).

B deficiency in conditions of water deficit could be due to a de-creased microbial population that is able to release B, making it available to plants and/or due to a decreased mineral dissolution, among others. B deficiency can aﬀect water relations in plants in dif-ferent ways: i) by altering water uptake in the root, ii) transport through the shoot and iii) loss of water in the leaf ([Wimmer and Eichert,](#page7) [2013](#page7)). An assay with Norway Spruce plants (Picea sp.) was performed, which included well-irrigated seedlings and seedlings exposed to two periods of drought with a period of rehydration at the end of the ex-periment and two B treatments (one of toxicity and another of defi-ciency). At the end of the experiment, the well-irrigated seedlings with B deficiency had visible symptoms of damage in the upper stems. The seedlings subjected to two cycles of drought with B deficieny showed reduced growth and content of P, Ca2+ and Mg2+. The lack of visible symptoms at low levels of B were probably related to a reduction in the absorption and transport of B due to two cycles of drought ([Möttönen](#page7) [et al., 2005](#page7)). In turnip plants (Brassica napa L.), the combination of B stress (with low and normal supply of B) and two irrigation treatments (adequate irrigation and drought) was also studied. In this case, a greater reduction of leaf and root dry biomass was found in those plants grown under B deficiency and in drought conditions. Also, drought reduced the content of B by approximately 70 % and 82 % of the plants with a normal supply of B and with B deficiency, respectively. In drought conditions with an adequate supply of B, the stomatal limita-tion was the most important cause of a net photosynthetic rate of 17 %; however, in the B and water deficient plants, the stomatal limitations, as well as the non-stomatal limitations, were involved in a reduction of 53 % in the photosynthesis rate. The explanation was that in-dependently of the B supply, water deficit damaged photosystem II ([Hajiboland and Frahangui, 2011](#page7)).

2.3. Excess of light

Light is essential for the growth and development of plants, but in excess it can be damaging. If the light energy absorbed that reaches the reaction centers (photosystem I and photosystem II) exceeds the quantity of energy that can be used, it can lead to damage to the leaf’s photosynthetic apparatus. This phenomenon, known as photo-inhibi-tion, can aﬀect the production of crops in field conditions. Also, a light intensity that overcomes the level of adaptation of the plants, combined with other stress-causing factors, can cause a greater photo-inhibitory eﬀect, as it occurs under B toxicity ([Table 1](#page7)). Thus, in cowpea plants (Vigna unguiculata L. Walp. P152), grown under high irradiation (1900 μmol m−2 s-1) and diﬀerent levels of B (0, 0.5 and 50 ppm), the photoinhibition was less in B-deficient leaves ([Inbaraj, 2011](#page7)). In other crops (Vigna mungo, [Noppakoonwong et al., 1993](#page7); Helianthus annuus, [Cakmak et al., 1995](#page7); Pelargonium × hortorum, [Mishra et al., 2009](#page7)), a reduction of light was shown to decrease the negative eﬀects produced by a B deficiency. In a study with geranium plants (Pelargonium × hortorum) grown with diﬀerent B concentrations that ranged from de-ficiency to toxicity (4.5, 45 and 450 μM of B) with three diﬀerent light intensities (100, 300 or 500 μmol m−2 s-1 PAR), [Mishra et al. (2014)](#page7) showed that the high irradiation induced a series of protective re-sponses in plants related to the carbon/energy status balance, rather than on tissue B content or B uptake, which reduced the negative physiological eﬀects caused by B stress (deficiency and toxicity).

2.4. Excess of CO2 concentration

It has been verified that a higher concentration of CO2 can result in greater vegetative growth in plants, as it increases photosynthesis and decreases transpiration in crops. These two factors can lead to a de-crease of the concentration of nutrients in plant tissues. Based on this, [Mishra et al. (2012)](#page7) planned an experiment to test the hypothesis that plants grown in elevated CO2 levels could intensify the eﬀects of B deficiency in conditions of B deficiency, while the eﬀects due to B toxicity would be reduced ([Table 1](#page7)). To conduct this experiment, ger-anium plants (Pelargonium × hortorum), barley (Hordeum vulgare), and water fern (Azolla caroliniana) were used. The plants were grown with three concentrations of B (4.5, 45 and 450 μM) and two CO2 con-centrations (370 and 700 ppm). Morphological parameters and gas exchange, B concentration in plants, and the protein concentration of the B transporter BOR1 were measured. The data indicated that the high concentration of CO2 worsened the eﬀect of B deficiency, as ex-pected, but did not improve the negative eﬀects due to B toxicity. Thus, the authors suggested that in the future, problems due to B stress could be worse than the present day. Also, the possibility that the expression of BOR1 and NIP5:1 proteins could change in elevated CO2 conditions was explored, which could aﬀect B absorption through the root. The results showed that the relative accumulation of BOR1 and NIP5:1 was not only influenced by the B content in the root, or the root zone as expected, but it was regulated by other environmental factors, as well ([Mishra et al., 2018](#page7)).

2.5. Excess of heavy metals

Heavy metals are naturally present in soils, but in the last few years, an anthropogenic accumulation of cadmium (Cd), Al, B, mercury (Hg), nickel (Ni), and lead (Pb) has been occurring due to industrial and agricultural activity, and the accumulation of every type of residue, which can result in several toxicities in crops. Al toxicity is a main problem especially in the tropics where abundant rainfall favors soil acidification by washing out alkaline earth elements from the rooting zone. These conditions also favor the loss of B from the soil. Therefore, Al-toxicity and B-deficiency are the most common interaction studied in plants in tropical and subtropical areas. In Al-sensitive plants species, B deficiency exacerbated the Al toxicity, as this deficiency leads to an increase in unmethylated pectin, which creates additional binding sites for Al in the cell wall as observed in Phaseolus vulgaris ([Stass et al.,](#page7) [2007](#page7)).

On the other hand, in Al-accumulator plants, the presence of Al in plants deficient in B mitigates the negative eﬀects of this scarcity. In tea (Camellia sinensis) plants, an Al-induced amelioration of B deficiency was found, attribute to the up-regulation of C and N metabolism and activation of the antioxidative defense by Al. In a study on the inter-action of B deficiency with Al in tea plants, with Al (0 and 300 μM) and B (adequate B supply, 46 μM B, and deficient supply) treatments, it was found that Al improved plant growth under B deficiency. This positive Al eﬀect in plants with B deficiency was related to an Al-induced in-crease of B contents in the root cell walls ([Tadeo and Gómez-Cadenas,](#page7) [2008](#page7)).

2.6. Extreme temperatures

Stress due to extreme temperatures (high and low temperature) is an environmental factor that aﬀects the growth and development of crops. The high temperature induces changes in the water relations and the accumulation of compatible osmolytes, decreases photosynthesis, produces hormonal changes and aﬀects the thermostability of the cel-lular membrane. The resulting deterioration of the plant (burning of leaves, branches and stems, senescence and leaf abscision, inhibition of shoot and root growth) and its reproductive parts (decrease in the de-hiscence of anthers and the pollen tube elongation) lead to a reduction

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of the the crops’ production. These damages are associated with a rapid production and accumulation of ROS that negatively aﬀect the cell’s metabolism. The mechanisms of adaptation to high temperature stress are: i) physiological alterations (accumulation of compatible osmo-lytes); ii) morphological alterations (reduction in the cell’s size, closing of stomata, increase in the density of stomas and trichomes and larger xylem vessels) and iii) biochemical alterations (increase in the anti-oxidant activity) ([Waraich et al., 2012](#page7)).

The low temperature in the root zone reduces the absorption of B and its eﬃcient distribution/utilization in the aerial part. The nature of this interaction depends on the plant’s tolerance to the cold, the manner in which cold treatments are applied (sharp or gradual decline) and the growing conditions (light intensity or relative humidity). In species sensitive to the cold, a root temperature between 10 and 17 °C de-creases the absorption of B and its use in the aerial part, and increases the leaf/root ratio. The tolerant crops require much lower temperatures (2−5 °C) to show the same responses. The B deficiency increases the damage to leaves due to the cold ([Huang et al., 2005](#page7)).

3. Boron application for ameliorating abiotic stress

In addition to the toxicity and deficiency of B, its chemical nature aﬀects a wide variety of biological functions in the plants which can help the plant cope with abiotic and biotic stresses. There is much evidence that B can alleviate the damages in plants grown under ex-treme conditions. From the literature, it is obvious that salinity, drought, Al excess, and biotic stresses can be alleviated by B applica-tions.

The application of B has been found to alleviate the adverse eﬀ ects of salinity on plant growth, yield and nutrient uptake. It is well known that B plays a critical role in carbohydrate metabolism and transport, while carbohydrate changes under salt stress are of great importance because of their relationship with processes such as photosynthesis and respiration. Moreover, due to the involvement of B in cell wall synthesis and structure, membrane structure and function, its application miti-gates the negative eﬀects of salinity through the maintenance of cell wall elasticity and the recovery of K + levels. Also, it has been well established that a B supplementation recovers nutrient balance and increases salt-tolerance of the nitrogen-fixing legume plants ([Marschner, 2012](#page7)).

Commonly, crops suﬀering drought stress have also shown B defi-ciency, as the supply of B is limited due to a reduction in water flow to the roots. Moreover, increasing evidence suggests that the mineral nutrient status of plants plays a critical role in increasing plant re-sistance to drought stress ([Marschner, 2012](#page7)). Interestingly, B nutrition has been found to increase the resistance of plants to drought stress by improving sugar transport, photosynthetic eﬃciency, hormone synth-esis, lipid metabolism, flower retention, pollen formation, seed and grain production and seed germination. Moreover, B-nutrition rich plants have shown an elevated resistance to drought stress due to in-creased water uptake from the soil rhizosphere by producing more root hairs and mycorrhizae. The nutritional status of the micronutrients B, zinc (Zn) and manganese (Mn) may aﬀect drought sensitivity of plants in two ways. Firstly, Zn, B, and Mn are involved in detoxification of ROS and in this respect may play a protective role in preventing pho-tooxidative damage catalyzed by ROS in chloroplasts. Secondly, these micronutrients may contribute to drought-stress tolerance by protecting against oxidative damage of membranes. In particular, the tolerance mechanism to water deficit was coupled to increases in total glu-tathione and ascorbate, which aimed to control the overproduction of hydrogen peroxide and to alleviate the negative consequences of elec-trolyte leakage in the plasma membrane and the impairment of gas exchange. The application of B in drought conditions has been shown to improve the nutritional status and production of the plant ([Table 2](#page7)) ([Rufat and Arbonés, 2006](#page7); [Wróbel, 2009](#page7); [Da Silva et al., 2015](#page7)).

In acidic soils, Al toxicity is one of the major limiting factors for crop

|  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Reference | [Karimi and Tavallali,](#page7) | [2017Diaz et al., 2011](#page7) | photosynthesisanduseofosmo-regulators(prolineandsoluble | [Rodríguez-Hernández](#page7) | [et al., 2013](#page7) | [Abid et al., 2014](#page7) |  | [Da Silva et al., 2015](#page7) | ®wasappliedwithsorbitol(AJIFOLSMBoron) |  |
|  | Cause | ImprovegrowthandCO | ReducethemovementofNa | sugars)Improvegrowthoftheaerialpartandroot,hydraulicconductance | oftherootsandmembranestability.DecreaseofPIP1proteins | Improveseedandstrawyield |  | Improvetreenutrition.NutrientassimilationwashigherwhenB |  |
|  |  | assimilation | to the leaves and increase the rateof |  |  |  |  |  |  |  |  |
|  |  | + |  |  |  |  |  |  |  |  |
|  |  | 2 |  |  |  |  |  |  |  |  |  |
|  | Levelofstress | 800,1600,2400and3200mg kg | soil75and150mMNaCl |  | 80mMNaCl |  | ECofsaturatedsoilpasteextract; | 4.dSm62 | fi25%eldcapacity |  |  |
|  |  |  | Irrigation water |  |  |  |  | −1 |  |  |  |
|  |  |  | . |  |  |  |  |  |  |  |  |
|  |  |  | −1 |  |  |  |  |  |  |  |  |
|  |  | (boricacid). Irrigation | (boricacid).Nutrient |  | (boricacid).Nutrient |  | .Disodiumtetraborate | B | Foliarapplication |  |  |
|  |  | −1 |  |  | 2 | −1 |  |  |
|  |  |  |  |  |  |  |  | O) |  |  |  |
|  |  |  |  |  |  |  |  | 2 |  |  |  |
|  |  |  |  |  |  |  |  | ·5H |  |  |  |
|  |  |  |  |  |  |  |  | 7 |  |  |  |
|  |  |  |  |  |  |  |  | O |  |  |  |
|  | BApplication | 05.mgkgsoil | water20mgL | solution | 1.mgL8 | solution | 2kgBha | 4 | 0.BmgL43 | ®AJIFOLSMBoron |  |
|  | pentahydrate(Na |  |
|  |  |  |  |  |  |  |  |  | . |  |  |
|  |  |  | −1 |  | −1 |  | −1 |  |  |  |  |
| ameliorating abiotic stresses. | Crop | ‘ ’Pistachio(Pistaciavera)cvBadami | Tomato (Solanum lycopersicum) var. | ‘ ’Ponchonegro | Broccoli (Brassica oleracea L. var. | itálica) cv Naxos | Canola (Brassica napus L.) Hyola, | Punjab Sarsoon and Bulbul | Eucalyptus (Eucalyptus urophylla x | E.Grandis) |  |
| Table 2BoronAplication for | Stress | Salinity |  |  |  |  |  |  | Drought |  |  |

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| [Wróbel, 2009](#page7) | [Rufat and Arbonés, 2006](#page7) | [Ye et al., 2003](#page7) | [Huang et al., 1996](#page7) | [Shahid et al., 2018](#page7) | [Favaretto et al., 2007](#page7) |  | toxicity, as B addition is |  |  |
| Improve grain and straw yields | Improve yield | Improve growth, root/shoot, B uptake and translocation | Improve grain set | Improve yield | Increase the root and shoot growth and root distribution in the soil | fiprole | candidate for the improvement of soil acidity and subsequently Al |  |  |
| fi40and60%eld capacity | . Dryland in the Mediterranean area | 10 °C in roots | 21. °C, Night temperature3 | 37. °C6 | 46. % Aluminum saturation5 |  | acidic soils, B could be a practical | carbonate, liming). |  |
| Wheat(Triticumaestivum)cvIsmena7cm | B) | FoliarapplicationμTemperatureOilseedrape(Brassicanapus)5.MH0 | μWheat(Triticumaestivum)cvSW4110MH | Rice(Oryzasativa)2kgBha | AluminumtoxicityArrowleafclover(Trifolium0.kgha25 | vesiculosum) | IfthehypothesisthatanincreasedamountofBcouldimproveAltoxicityinmostcropsunder | comparativelylessexpensivethanexistingapproachesofsoil-acidityamendments(calcium |  |
| applicationintilleringphaseAlmond(Prunusdulcis)7Ltree |  |
| (0.H3% | ppmBSolubor(20.8% | 3 | 3 |  | ofB(boricacid) |  |  |  |  |
| ). Foliar |  | solution | solution |  |  |  |  |  |  |
| BO |  |  |  |  |  |  |  |
| 3 |  |  |  |  |  |  |  |  |  |
| 3 |  | Nutrient | Nutrient |  |  |  |  |  |  |
| −1 | 832 | . | . |  |  |  |  |  |  |
| BO |  | 1 |  |  |  |  |
| BO |  |  |  |  |  |
| plant | −1 | 3 | 3 | −1 | − |  |  |  |  |
| 3 |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |

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productivity around the world, and approximately 50 % of the world’s total land area is comprised of soils with a pH ≤ 5. Whereas in mildly acidic or neutral soils Al exists primarily in the insoluble forms and is biologically inactive, in acidic soils Al becomes soluble and toxic to plants. Al is assumed to exert its toxic eﬀect in the apoplast through the interaction with the negative binding sites of the cell walls, primarily pectin from the root epidermal and cortical cells. Moreover, Al is likely to occur as Al(OH)3 inside the plants, which is structurally similar to B (OH)3. Therefore, Al-toxicity has been proposed to exert its toxic eﬀect by inducing B-deficiency. B-induced alleviation of Al toxicity has long been confirmed in several reports, by reduced uptake and mobilization of Al ions and by eliminating oxidative stress and root injuries. An abundant B supply can promote the immobilization of Al in alkali-so-luble pectin by enhancing de-methylesterification and the increase of pectin RG-II in alkali-soluble pectin has been suggested. In addition, B suppresses the entry of Al into the symplast, thus alleviating Al toxicity in epidermal root cells ([Riaz et al., 2018a](#page7), [b](#page7); [Yan et al., 2018a](#page7), [b](#page7); [Yan](#page7) [et al., 2018c](#page7)). On the other hand, B has been shown to improve the response of orange trifoliata to Al toxicity by regulating the metabolism pattern of amino acids and carbohydrates ([Yan et al., 2019](#page7)). If the hypothesis that an increased amount of B could improve Al toxicity in most crops under acidic soils is proven, B could be a practical candidate for the improvement of soil acidity and subsequently Al toxicity, as B addition is comparatively less expensive than existing approaches of soil-acidity amendments (calcium carbonate, liming).

Extreme temperatures are one of the abiotic stresses that causes a decrease in worlwide production of crops. B, as it plays an important role in the structure of the cell wall, sugar translocation, and the re-productive state of plants, is essential for alleviating the damage pro-duced by this stress ([Waraich et al., 2012](#page7)). In an experiment conducted for evaluating the use of B with tolerance to high temperatures in rice, it was found that the application of 1 and 2 kg B ha−1 reduced the ne-gative eﬀects of a high temperature of 37.6 °C in the vegetative and reproductive stages, as the exogenous application of B had a substantial eﬀect on the stability of the cellular membrane, the mobilization of sugars, the viability of pollen and the fertility of the spikelets ([Shahid](#page7) [et al., 2018](#page7)). In wheat, a treatment with 10 μM H3BO3 in the nutrient solution improved the seed set when a high nightime temperature was used (21.3 °C) ([Huang et al., 1996](#page7)).

4. Conclusions and future perspective

Boron (B) is an essential nutrient for vegetative growth, re-productive development, production and quality of the crops. The quantities of B needed are small, and any imbalance between its availability and need can cause problems. In plants, the content of B depends on the transpiration stream, although in certain concentration ranges in the soil, the plants have developed mechanisms and strategies to avoid damage due to toxicity or deficiency. Recent research has pointed that these mechanisms are related to the regulation of selective B transporters (BOR) and plasma membrane intrinsic proteins (PIP), activation of antioxidant systems, and distribution of B at the cellular level. The interaction of B with other stresses is very complex, as many factors come into play, such as transpiration, B chemistry in plants, damage caused in the plant by other stresses, etc. In most of the ex-periments, a negative interaction was found in which the simultaneous combination of stresses was more harmful than the individual stresses, even though the combination of stresses resulted in B levels that were more acceptable than those obtained without this interaction. This in-dicates that plants, when facing adverse soil and climate conditions, become more sensitive to B stress. To help growers cope with si-multaneous stress problems related with B stress, researchers should study the underlying mechanisms of B stress tolerance to understand their modes of interaction with other abiotic stresses. The creation of knowledge at the basic level, such as conducting experiments in com-mercial conditions, analyzing a high range of stresses with diﬀerent

concentrations of B, will be useful for the design of novel agronomic strategies and to optimize the management of crops with the aim of palliating the negative eﬀects of the simultaneous combination of stresses, thereby increasing the resilience of crops to climate change. On the other hand, in the last few years numerous scientific evidence have been brought to light that the controlled application of B could be an appropriate practice for decreasing the sensitivity of crops to abiotic stresses such as drought, salinity or heavy metal toxicity.

CRediT authorship contribution statement

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Declaration of Competing Interest

No interests to declare.

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