Boron – a critical nutrient element for plant growth and productivity with reference to temperate fruits

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The exciting developments in boron research in the past few years greatly contributed to better understanding of the role of boron in plants. Isolation and characterization of the boron–polysaccharide complex from cell walls provided the first direct evidence for boron crosslinking of pectin polymers. Inhibition and recovery of proton release upon boron withdrawal and restitution in plant culture medium demonstrated boron involvement in membrane processes. Rapid boron-induced changes in membrane function could be attributed to boron-complexing membrane constituents. Molecular studies of boron nutrition have been initiated by the discovery of a novel mutant of *Arabidopsis thaliana* with an altered requirement for boron. Besides this, boron fertilization regardless of application mode increases pollination, fruit set, fruit yield and quality of temperate fruits. Moreover, it enhances the marketable fruit yield of many fruits by decreasing physiological disorders to a great extent. Positive responses to boron application throughout the world provides clear evidence of boron deficiency. Climate, particularly high light intensity and low temperature are factors that need to be considered in relation to the occurrence of boron deficiency. Boron deficiency can be readily prevented and corrected by both soil and foliar applications.

Keywords: Boron, fruit quality and yield, photosynthesis, pollination, respiration.

A GLANCE at the history of agriculture reveals that man has always depended on plants for his existence on this planet. The period from immemorial times during which man began cultivation of plants marks the dawn of agriculture. Since then man has been improving the productivity efficiency of plants through materialistic adjustments. The revelation of the existence, activity and benefits of mineral nutrients is indeed an important milestone towards modern agriculture and has created a subject of great interest for plant researchers. Contributions in this direction have unfolded several facts about the physiology of nutrition. The growing knowledge of mineral nutrition of plants with special reference to micronutrients has made us realize that great changes are possible through judicious supply of certain inorganic substances.

Micronutrients, also called as trace elements, are the essential nutrients which are required in small quantities for the growth of plants. These elements are: iron (Fe), manganese (Mn), zinc (Zn), copper (Cu), boron (B), molybdenum (Mo), nickel (Ni) and chlorine (Cl) (ref. 1).

The terms 'micronutrient' and 'trace element' do not imply that these nutrients are somehow less important than macronutrients. On the contrary, the effects of micronutrient deficiencies can be severe in terms of stunted growth, low yields, dieback and even plant death. Moreover, very small application of micronutrients may produce dramatic results[2].

The importance of micronutrients has been realized during the past four decades when widespread micronutrient deficiencies were observed in most of the soils where intensive agriculture is practised. The reasons for increased attention towards micronutrient deficiencies are summarized as under:

(i) Crop yields have been increased by intensive plant production practices, which has resulted in greater removal of micronutrients from soils[1,2].

(ii) Use of micronutrient-free-high analysis fertilizers in modern agriculture[1,2].

(iii) Increased knowledge of plant nutrition and improved instrumentation techniques has helped in the diagnosis of micronutrient deficiencies in soils, which formerly might have gone unnoticed[1,2].

(iv) Increasing evidence indicates that food grown on soils with low level of trace elements may provide insufficient human dietary levels of certain elements, even though the crop plants show no signs of deficiency themselves[2].

The deficiency of boron occurs worldwide[3]. Sparr[4] has also observed that boron deficiency is one of the most common among plant micronutrient deficiencies worldwide. Keeping these findings in view the role of boron in temperate fruits is reviewed in this article.

Boron

The essentiality of boron as a micronutrient for plants was provided by Warington[5], who not only showed that field bean (*Vicia faba*) died when boron was not supplied in the nutrient solution, but also that boron was needed for revival. Many researchers presented data to show that boron was needed for the growth of crops. However, none of the reports before Warington's[5], satisfied the conditions of essentiality that were subsequently laid down by Arnon and Stout[6] even Warington's study did not show that the role of boron could not be replaced by another element or that boron was directly involved in plant metabolism.

Sites of boron action in plant metabolism

Primary cell-wall structure and membrane function are now closely linked to boron nutrition. In contrast, the role of boron in plant metabolism is still a subject of considerable debate. Focusing on the diversity of early responses to boron deficiency, Lovatt and Dugger[7] postulated that boron can be involved in a number of metabolic pathways and can act in the regulation of metabolic processes similar to plant hormones. However, due to lack of suitable information, boron function in metabolic events has never been properly evaluated. There is substantial evidence supporting the association of boron with ascorbate metabolism. One way boron could increase ascorbate concentration is through its effect on the plasma membrane electron transport reactions. Barr and his associates[8,9] showed that boron instantaneously stimulated the auxin-sensitive plasmalemma NADH oxidase. This enzyme, also called as ascorbate free radical oxidoreductase[10], catalyses the transfer of electrons to the ascorbate free radical. Inhibition of this process in the absence of boron could result in the deprivation of reduced ascorbate. Another site of boron action that is not connected with a structural role in cell walls or membranes is auxin metabolism. Boron interaction with auxin has long been postulated, and although the issue remains controversial, it may be central to our understanding of the role of boron in plants. Bohnsack and Albert[11] demonstrated a 20-fold increase in indoleacetic acid (IAA) oxidation rate in root apices 24 h after boron was withheld from the nutrient medium. The authors attributed the increase to stimulation of the activity by high levels of IAA accumulated in boron-deficient tissues.

Role of boron in physiology of plants

Cell-wall structure

An important factor determining cell size and shape during plant development in higher plants is the primary cell wall. Over the years, a close relationship has been observed between the primary cell wall and boron nutrition[12]. Up to 90% of the cellular boron has been localized in the cell-wall fraction[13] where it is associated with pectinacious compounds[14]. Hence, the first symptoms of boron deficiency include abnormalities in cell wall and middle lamella organization[13]. Boron performs a physical role in maintaining cell-wall extensibility and under boron-deficient conditions the cell wall becomes rigid, inelastic and brittle[15]. Formation of borate esters with hydroxyl groups of cell-wall carbohydrates and/or glycoproteins has been proposed as a mechanism for crosslinking cell-wall polymers[13]. Borate bridging could explain many of the characteristics of boron-deficient and boron-toxic plants. This type of bonding could account for brittle leaves of boron-deficient plants, whereas plants grown with supra-optimal levels of boron produce leaves that are plastic or elastic in their response to bending[13].

Membranes and membrane-associated reactions

The evidence provided by cell-wall studies explains many problems caused by boron deficiency. However, there are some aspects of plant boron nutrition that go beyond cell-wall structure. These include rapid changes in membrane function induced by addition of boron to boron-deficient tissues. Boron was first localized in maize root membranes by Pollard *et al.*[16] and was later found in membrane fractions from protoplasts of mung bean by Tanada[17]. Boron plays an important role in maintaining plasma membrane integrity[18], possibly by linking glycoprotein and glycolipid components of the plasma membrane bilayer through its ability to complex OH-containing polysaccharides[19] or through its involvement in enzyme systems such as ATPases[18] or esterases[20], that become active on pollen hydration. Although the quantity of boron in membranes was not large, especially compared with that in cell-wall fractions, it was significant for ion uptake. Lawrence *et al.*[21] showed lower ATPase activity in plasmalemma-enriched vesicles from boron-deficient chickpea roots than in vesicles from control roots. Obermeyer *et al.*[22] reported boron stimulation of the plasmalemma ATPase from ungerminated pollen grains of lily. Barr and Crane[8] showed that addition of exogenous boric acid (with or without 2,4-dichlorophenoxyacetic acid) to low-boron cells caused an instantaneous stimulation of the plasma membrane NADH oxidase, which was the fastest boron response reported. By stimulating NADH oxidase, boron could be involved in keeping ascorbate reduced at the cell-wall/membrane interface. It is noteworthy that both NADH oxidase activity and ascorbate have been linked with plant growth processes[10,23]. Thus, boron treatment of low-boron plants stimulates ATPase activity, NADH oxidase activity and ion transport[8]. Though these changes are associated with membrane function, several researchers have

speculated that boron may be affecting physical properties of membrane proteins. Shkolnik[24] observed that several enzymes, normally bound to membranes or walls in a latent form, become active when released under boron-deficient conditions. These enzymes include ribonuclease, glucose-6-phosphate dehydrogenase, phenylalanine ammonia lyase, β-glucosidase and polyphenoloxidase. Release of these enzymes under boron-insufficient conditions could severely alter plant metabolism, deplete RNA and increase phenolic synthesis. Many of the phenolics are potent growth inhibitors[25]; the same phenolics also inhibit ion uptake and thus retard membrane function[26].

Reproduction, pollen tube growth and pollen germination

Cell-wall composition may be of primary importance in determining the quantity of boron required for growth. However, it has been observed that in most plant species the boron requirement for reproductive growth is much higher than for vegetative growth[13]. Boron may be involved in carbohydrate or phenolic metabolism which is central to pollen tube growth[15]. Loewus and Lambarca[27] provided evidence that boron influences incorporation of D-glucose ^{14}C into pollen tube walls and may play a crucial role in pollen tube growth. Boron requirement for reproductive growth in plants has long been recognized. Schmucker[28] proposed that boric acid was bound to hydroxyl-rich organic molecules like sugars and was involved in pollen tube wall formation. Lewis[29] suggested that boron retards phenol oxidation during pollen tube growth, thereby protecting pollen membranes from attack by free radicles generated by phenol oxidation. Degradation of pollen tube membranes would be expected to lead to an increase in the number of burst tubes that occurred in the boron deficient *in vitro* cultures[15]. Pollen grains of most species are naturally low in boron, but in the style, stigma and ovary boron concentration is generally high[30]. Visser[31] showed that continuous and ample supply of boron was required for pollen tube growth and speculated that boron was complexing with cellular materials during the tube elongation process. Johri and Vasil[32] demonstrated that boron was more critical for pollen tube elongation than for pollen germination. Rapid growth of pollen tube depends on constant fusion of vesicles forming the plasmalemma and continuous secretion of cell-wall material. Whatever the mechanism, the role of boron in reproductive growth is particularly striking. The uniformly high boron requirement for reproductive growth across the plant kingdom is intriguing and indicates similarities between reproductive structures, so unlike cell walls; perhaps the composition of the pollen tube wall is similar across plant species. Gauch and Dugger[30] have quoted Lohnis[33], who has mentioned that 'it is quite conceivable it will be the study of pollen which may elucidate the very fundamental part boron plays in the biochemical processes'.

Role of boron in temperate fruits

Effect on photosynthesis

Wójcik *et al.*[34] observed that foliar boron spray has no effect on boron status in leaf and fruit tissues, indicating that absorption rate of foliar applied boron and/or re-translocation of boron in plant is limited (Table 1). Besides, phloem boron mobility in apple is good[35]; it seems that a lack of the effect of foliar boron sprays on boron level in leaf was related to restricted boron absorption rate by spur leaves. This is possible because spur leaf area of the apple tree at the beginning of the growing season is small[34]. Hence early-season boron spray has little or no effect on summer leaf boron concentration of apple trees. These results were in agreement with the findings of Bramlage and Thompson[36], and Khalil and Thompson[37]. Contrary to these results, Peryea *et al.*[38] showed increased mid-season leaf boron status as a result of pre-bloom boron sprays. The opposite results of the above two studies on the effect of foliar boron sprays on mid-summer leaf boron status could be due to different soil properties affecting the behaviour of boron in the soil and consequently its uptake by the plants[34].

Table 1 also shows increase in net photosynthetic rate which may be attributed to the increase in chlorophyll content of the leaves. Moreover, soil boron application increased the activity of catalase and glutathione reductace, which act as antioxidants thus saving the electron transport mechanism of the plant from getting oxidized by free radicles like superoxide radicles, singlet oxygen radicles, etc.[34].

Thurzo *et al.*[39] observed an increase in the photosynthetic pigment contents like chlorophylls and carotenoids by foliar application of boron in sweet cherry at full bloom. Due to this, the increase in the rate of photosynthesis is inevitable (Table 2).

Effect on respiration in temperate fruits

There is generally less literature concerning the influence of boron on fruit respiration. Besong and Lawanson[40] confirmed that the activity of respiratory enzymes was intensified under boron deficiency, but lowered by boron application. Ethylene production in boron-treated fruit was reduced, most effectively after boron + calcium application. The functions of boron and calcium on the structure of cell walls and cell membranes are well known[41]. Calcium and/or boron can maintain cell compartmentation so that the formation of ethylene could be less during the ripening of boron-treated fruit. Another possibility might be that the formation of methionine, a precursor of ethylene, is affected by boron.

Table 1. Effect of boron on leaf boron concentration, photosynthesis and enzymatic changes in leaves of apple trees (modified after Wójcik *et al.*[34])

Treatment	Leaf boron concentration (mg/kg)	Leaf chlorophyll content (mg/g DW)	Net photo-synthetic rate ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)	Stomatal conductance ($mol\ m^{-2}\ s^{-1}$)	Activity in (unit/mg) of		
					Catalase	GR	SOD
Soil boron application (2 g/tree)	42b	2.03b	12.2b	0.20b	15.6b	3.7b	86a
Foliar boron application (0.03%) (4 times)	23a	1.51a	7.5a	0.11a	7.9a	0.09a	91a
Control	21a	1.42a	7.8a	0.09a	8.5a	0.06a	90a

GR, Glutothione reductase; SOD, Superoxide dismutase. a, b, c means that figures with similar letters are statistically at par while as figures with different letters are significantly different.

Table 2. Effect of boron on photosynthetic pigment contents[39]

Treatment	Chl *a*	Chl *b*	Chl *a*/Chl *b*	Total chlorophyll	Total carotenoids	Total chlorophyll carotenoids
B1 (full bloom)	6.20c	1.89b	3.30ab	8.09c	1.44c	5.62bc
B2 (full and 5wafb)	1.50a	0.50a	2.99a	2.00a	0.37a	5.47b
Control	2.69b	0.74a	3.65b	3.43b	0.77b	4.43a
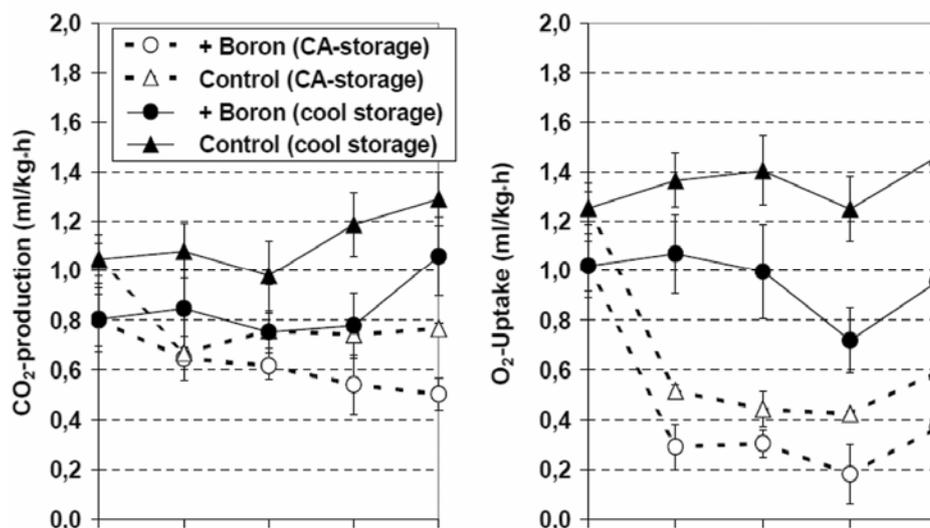
Figure 1. Effect of boron application on CO_2-production and O_2-uptake of conference pears stored for 5 months under cool (–0.5°C) and controlled atmosphere conditions (5% CO_2 + 2% O_2, –0.5°C); adapted from Xuan *et al.*[42].

Xuan *et al.*[42] observed that boron-treated fruit showed continuously lower O_2 uptake and CO_2 emission under controlled atmospheric conditions as well as under cool storage conditions (Figure 1). At the same time, it was noticed that O_2 uptake under controlled atmospheric conditions in boron-treated and boron-untreated fruits decreased more than the corresponding CO_2 emission. At harvest, no ethylene was found in all treatments (Figure 2). After one month of controlled atmospheric storage, the formation of ethylene started and increased till the end of 5-months storage period. At the same time, the boron and boron + calcium treatments produced less ethylene than the control fruit. The boron + calcium treatment always had the lowest rate of ethylene formation.

Effect of boron application on pollination of temperate fruits

Pollen tubes exhibit tip growth[43] by fusion of vesicle membranes originating from the endoplasmic reticulum and dictyosomes[44]. A possible role of boron in pollen tube growth may involve vesicle production, transport, fusion or the subsequent formation of the pollen cell wall. Pollen tube cell-wall precursors are rich in polypeptides, mostly glycoprotein and polysaccharides rich in arabino furanosyl residues[45]. Many of these compounds are known to form strong complexes with boron[13]. Most of cell boron is known to be located in the cell wall where it is associated with pectinaceous compounds[14]. Under

boron-deficient conditions, cell walls become rigid, inelastic and brittle. Boron may be involved in some of the biochemical/physiological events involved in pollen germination and tube growth.

Nyomora et al.[15] observed that within the first 48 h of pollination, when boron was applied to either of the tree parents, boron in pistil-donor trees was significantly more effective than boron applied only to the pollinizer trees (Figure 3). Low and moderate boron applied previously to the trees increased pollen germination and pollen tube growth respectively. The documented role of boron in cell-wall structure is consistent with a role of boron in pollen germination and growth, in which extensive cell-wall synthesis and expansive growth is a key process.

Lee et al.[46] concluded from their experiment of boron application on pear that although the addition of highest levels of boric acid (500 mg l^{-1}) into the medium resulted in a reduction in pollen tube growth to below control levels, moderate boric acid effected a significant enhancement of pollen germination and pollen tube growth in vitro (Figure 4). The role of supplemental boric acid was indicated by the enhanced in vitro pollen tube growth observed in boron-supplemented media[15,47].

Effect on fruit set, yield and fruit quality of temperate fruits

Boron is important in pollen germination and pollen tube growth, which is likely to increase fruit set[34]. Therefore, boron fertilization may increase yield, particularly when plants are grown on sandy soil with a low content of available boron, as shown by Wójcik et al.[34] and Nyomora et al.[48]. Although the mechanism of boron translocation within plants has not been well understood, the effect of boron fertilization to apple trees on fruit quality as altered by several biological and environmental factors such as cultivar, orchard location, rainfall and air temperature has been well known for many years[49,50].
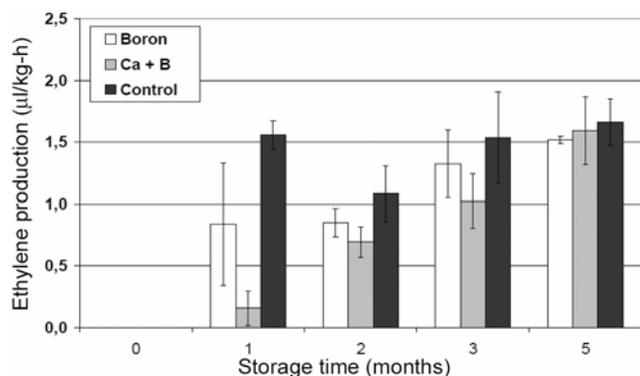

Figure 2. Effect of boron and boron + calcium application on ethylene production of 'conference' pears stored for 5 months under CA conditions (5% CO_2 + 2% O_2 at –0.5°C; adapted from Xuan et al.[42]).

Wójcik et al.[34] observed that pre-bloom foliar application of boron to apple trees increases fruit set as well as yield (Table 3). Moreover, soil application of boron also increases yield but to a lesser extent. The authors also explained the increase in yield of apple to increase in fruit size and fruit number through soil application and foliar spray of boron respectively.

Wójcik et al.[34] also reported an increase in total soluble solids as well as total acidity due to soil boron application. This can be attributed to transportation of higher amount of assimilates into fruit tissues. The results presented in Table 3 are in agreement with those of Westmark et al.[51], who found that boronic acids facilitated sugar transport through artificial lipid bilayer membranes.

Nyomora et al.[15] reported that the reciprocal crosses between pollinizer and pistil donor trees that received varying rates of boron showed higher initial fruit set percentages in comparison to crosses from non-treated trees, with the exception of crosses that involved combinations of nontreated trees and trees receiving highest rate of boron (Figure 5 a). Irrespective of the boron treatment in pistil donor trees, pollen from pollinizer trees treated with the control or highest rate of boron (0 or 2.5 kg ha^{-1}) had the lowest initial fruit set. Highest fruit set occurred in the treatment combination in which the pollinizer trees received boron at 0.8 kg ha^{-1} and the pistil donor trees received boron at 0.8–1.7 kg ha^{-1}. Likewise, boron at 0.8–1.7 kg ha^{-1} in both tree types gave the highest final set of 60–70% (Figure 5 b), whereas pollen from non-treated trees and from trees which had received the highest rate of boron resulted in the lowest final fruit set (40%).

Similarly, Wójcik et al.[52] reported that among boron treatments, only foliar boron application after bloom increased fruit yield in apples. Increase of fruit yield as a result of spraying boron after bloom was directly related to higher fruit setting. It should be noted that spraying with boron before bloom had no effect on fruit set and yield, which is generally contradictory to the results of Gu et al.[53]. These authors found increase in apple fruit setting as a result of leaf boron application before bloom. The lack of the effect of spraying with boron before bloom on fruit setting may result from limited movement of exogenous boron from spur leaves to flowers and fruitlets, as suggested by Wójcik and Mika[54]. According to Van Goor and Lune[55], an abundant yield of apple trees depends on high boron concentration in fruitlets during the first 5–6 weeks of development when intensive cell division occurs. In our experiment, the limited boron translocation from the soil and leaves to the fruits with soil boron application and boron spraying before bloom was probably related to competition between leaves and fruitlets for boron. Young leaves particularly accumulate boron, preferentially in spur leaves, which may have caused reduction of boron movement to the fruitlets[54]. Abd El-Fatah et al.[56] observed an increase in individual fruit weight as well as yield of persimmon by application of
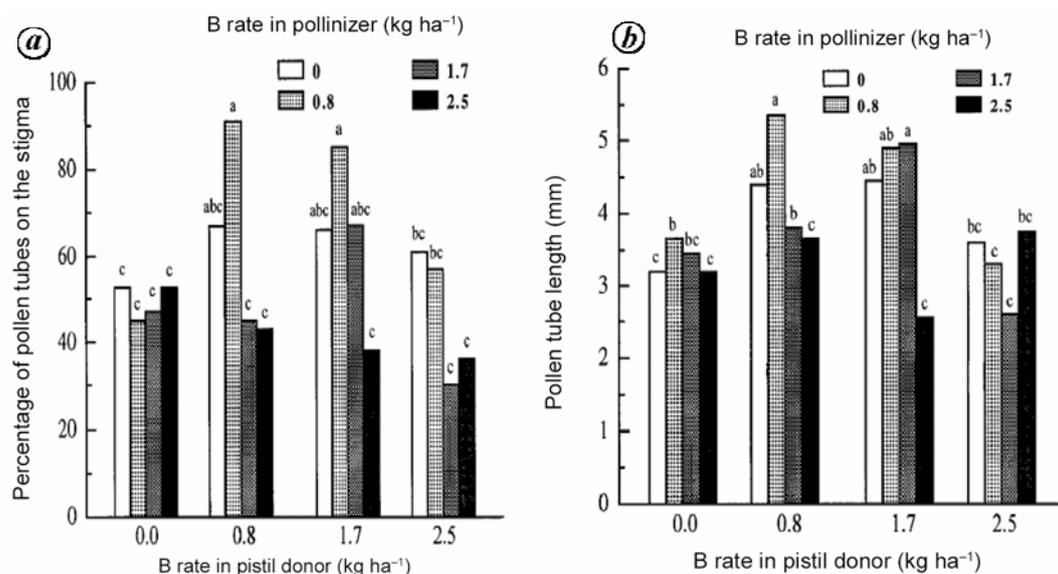
Figure 3. *a*, Percentage of pollen tubes on the stigma in almond. *b*, Pollen tube growth 48 h after pollination (adapted from Nyomora et al.[15]).
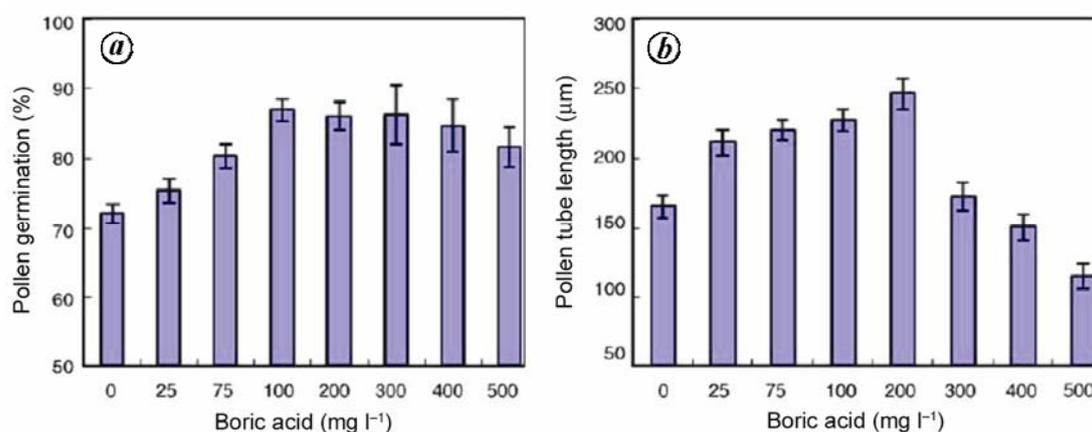

Figure 4. *a*, Percentage of pollen germination in pear. *b*, Pollen tube growth 48 h after pollination. (Adapted from Lee et al.[46].)

Table 3. Effect of boron on fruit set, yield and quality of apple (adapted from Wójcik et al.[34])

Treatment	Fruit set (%) DAF			Yield (kg/tree)	Mean fruit weight (g)	TSS (%)	Acidity (%)
	14	28	42				
Soil boron application	36.2a	15.3a	7.2a	4.3b	226b	13.6b	0.72b
Foliar boron application	40.2a	25.3b	15.2b	6.8c	191a	12.5a	0.65a
Control	39.4a	11.4a	6.9a	3.1a	188a	12.4a	0.63a

TSS, Total soluble solids.

boron. Singh et al.[57] observed an increase in marketable fruit yield of strawberry by foliar application of boron and/or calcium. Kamiloglu[58] concluded that adopting some cultural practices along with application of boron increases yield, cluster weight as well as berries per cluster. Usenik and Stampar[59] observed that increase in the

fruit set and yield of sweet cherry due to application of boron was not considerable when climatic conditions were not favourable for fruit set. Moreover, they also reported that different cultivars respond differently to boron application. Nyomora et al.[48] also reported cultivar differences to boron application in the yield of almond trees.
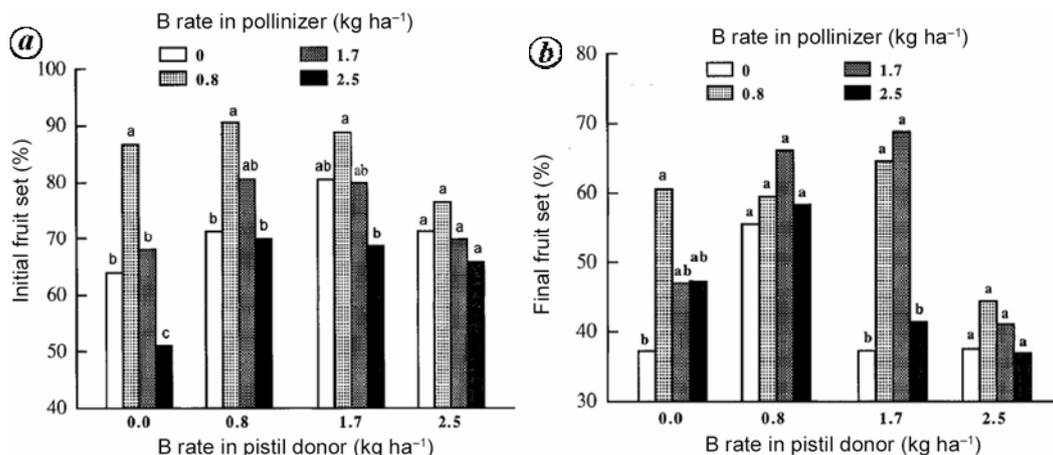
Figure 5. *a*, Initial fruit set (%). *b*, Final fruit set (%) adapted from Nyomora *et al.*[15].
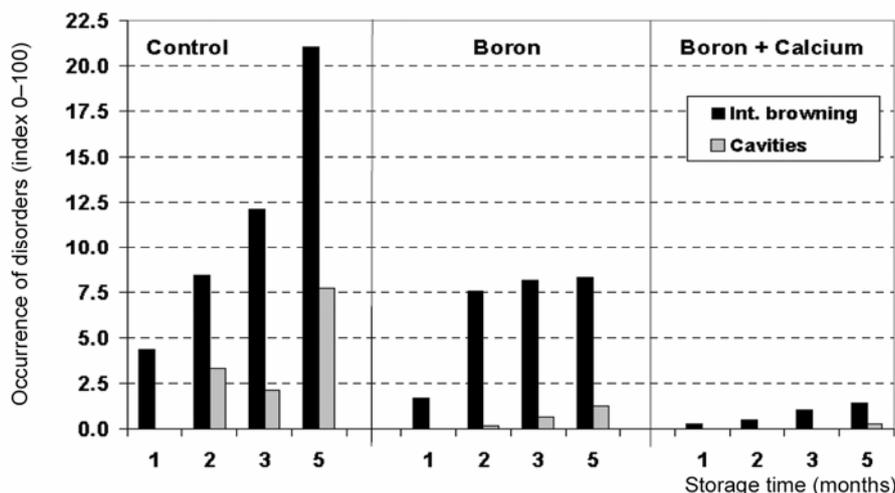

Figure 6. Occurrence of controlled atmosphere (CA) conditions-related disorders in boron and calcium-treated 'conference' pears during a 5-month CA-storage period at 5% CO_2 + 2% O_2 at –0.5°C.

Effect of boron in reducing physiological disorders of temperate fruits

Xuan *et al.*[42] concluded that pre-harvest boron application had a substantial effect on several physiological parameters and on the storability of pear fruit, i.e. boron may improve the ability of fruit tissue to better resist impaired storage conditions with the result of avoiding typical browning disorders (Figure 6). Presumably, treated fruit could reinforce the structure and integrity of the cell membrane, which may be impaired by high CO_2-stress conditions. It is well documented for different plants, that boron plays an important role both in structural and functional integrity of membranes, as well as in cell-wall formation[60]. The role of boron for improved membrane integrity of pears was demonstrated by Xuan *et al.*[61].

Christensen *et al.*[62] concluded that the fall foliar treatment had the lowest incidence and severity of boron deficiency symptoms in fruit (Figure 7). The other boron treatments (dormant soil, pre-bloom foliar and bloom foliar) also reduced fruit symptom incidence and severity, but not as effectively as the fall foliar treatment. Vine fruit response did not correspond directly with tissue boron levels. While fruit symptoms were reduced more effectively by the fall foliar than the pre-bloom foliar treatment, tissue boron levels were higher in the latter than in the former treatment. This may be due to the inability of the pre-bloom foliar spray to reverse some earlier effects of boron deficiency on primordial tissue in developing buds. Also, at pre-bloom, the calyptrae (caps) prevent the foliar spray from contacting the unexposed flower parts (anther, stigma, style and ovary). These calyptrae are shed at bloom, along with their spray deposits, finally exposing the flower parts to complete their pollination and fruit set. Singh *et al.*[57] observed that boron and/or calcium spray reduces fruit malformation, albinism as well as grey mould percentage in strawberry.
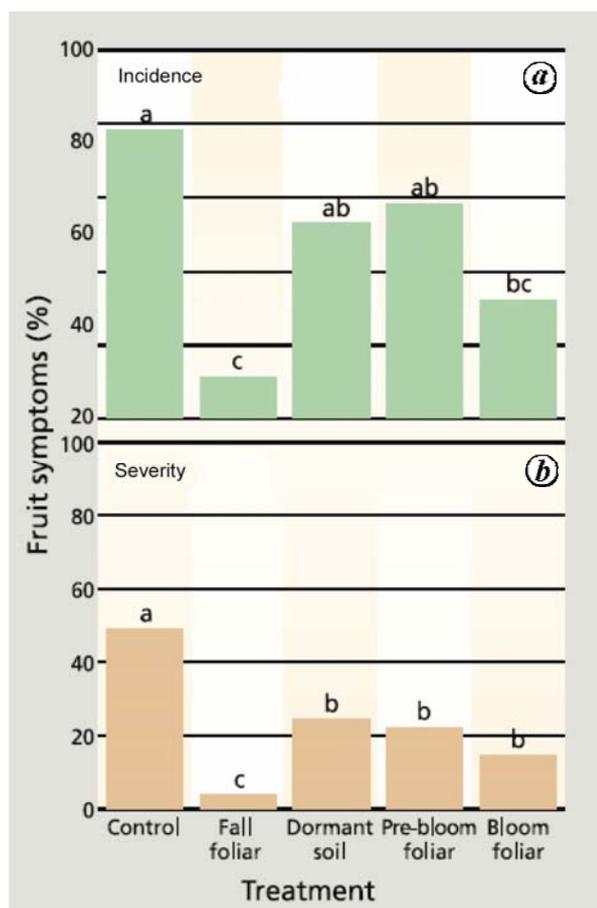
Figure 7. Effect of boron sprays at different stages on 'hen and chicken disease' in grapes.

Symptoms of boron deficiency

Boron deficiency is particularly prevalent in light-textured soils, where water-soluble boron readily leaches down the soil profile and becomes unavailable to the plants[63]. Boron deficiency may also occur in soil with adequate boron level, if its uptake is impeded by over liming, dry or wet soil conditions and a low level of soil oxygen[64,65]. Adequate boron nutrition is critical not only for high yields but also for high quality of crops. Boron deficiency causes many anatomical, physiological and biochemical changes, most of which represent secondary effects[12]. Boron is an essential nutrient required for higher plants[66]. It has been found to play a key role in reproductive processes affecting anther development, pollen germination and pollen tube growth[13,67]. For this reason, in boron-sensitive crops abortion of flower initials and poor set of fruit or seeds are observed under conditions of boron deficiency[68,69]. The primary effect of boron deficiency appears to be the disruption of the normal functioning of the apical meristems with changes in membrane structure, cell-wall synthesis, metabolisms of auxin, carbohydrate, ascorbate and RNA, and lignification, phenol accumulation and sucrose transport being secondary effects[12,19,70].

Apple (*Malus domestica* Borkh.) trees have been known to have high requirements of boron[3]. Poor fruit set and in turn reduced yield are the first visual signs of boron deficiency, since this nutrient plays a key role in reproductive growth[13,67]. Apples of boron-deficient trees are small, deformed, corked, sensitive to cracking and russeting, and have yellow skin with a poor red colour[71]. Under boron deficiency, apple fruits may also have low concentrations of soluble solids and acids[72].

Besides pomaceous fruits, stone fruits are also affected severely by boron deficiency. For example, boron-deficient cherry shoots grow for some time and then the tips die. Leaves are distorted in shape, with irregular serration, and may cup or roll downward. Under conditions of boron deficiency, splitting of the bark frequently occurs. Some buds of B-deficient plants may fail to open in spring, whereas others shrivel and die. Cracking, shrivelling, deformation, internal and external browning, and corking around the pit and in the flesh are signs of cherry fruit boron deficiency[73].

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