



Boron in arid zone agriculture: Israeli case studies

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ABSTRACT

Relatively high levels of boron (B) can be found in soils and irrigation water used for agriculture in semi-arid and arid regions. Furthermore, climatic conditions and resulting high levels of plant transpiration in dry regions intensify B uptake and accumulation in plants and increase the probability of B toxicity. The focus of this review is on B interactions with soils and plants in dry regions. A basic introduction to B in soils and solutions and to B in the soil-water-plant continuum is presented to provide the reader with sufficient background to understand issues of B in arid and semi-arid agriculture. Crops in arid areas are prone to exposure to stress-causing factors from excess B that occurs simultaneously with general salinity stress. In some cases in arid zone agriculture excess B is a result of native soil-born B, in other cases it is a result of B introduced with irrigation water. Both native and introduced B can have long-term consequences on crop growth and agricultural management. The nature of excess B-salinity interactions is also reviewed. Case studies representing two scenarios regarding excess B in arid agriculture are presented. In the first, naturally occurring B in vineyards in the Jordan Valley led to toxicity, even after years of leaching and irrigation with low-B water. In the second, saline water with high B concentration historically utilized in the western Negev for irrigation of cotton had serious repercussions on subsequent peanut crops. Crop and water management options appropriate to anticipated conditions of high B in arid agriculture are presented and discussed.

1. Introduction

Boron (B) is an essential micronutrient element required for the normal growth of plants. Plants vary in their B requirements, but the range between deficient and toxic soil solution concentrations of B is smaller than for any other nutrient element [1]. Boron deficiency is most likely in coarse textured soils in humid regions. B toxicity, however, resulting from high levels of B in soils and from additions of B via irrigation water, is common in arid and semi-arid regions [2]. The climatic conditions (high temperatures, low rainfall, low humidity, and high light intensity) and the resulting high levels of plant transpiration in the dry regions intensify B uptake and accumulation in plants and thus increase the probability of B toxicity.

Boron is taken up into plants from the aqueous soil solution and is largely a function of the solution's B concentration [2]. The concentration of B in soil solution is strongly affected by B-soil chemical interactions – primarily adsorption-desorption processes that are, in turn, affected by soil constituents and conditions [2].

The characteristics of typical arid and semiarid zone soils – that they can be saline, contain high natural levels of B, and have relatively low organic matter content – all affect soil B reactions and plant B uptake.

Boron toxicity in plants is a phenomenon encountered in many places throughout the world's arid regions. Specific cases of high B levels and toxicity to agricultural crops have been reported in South Australia [3], California [4], Israel [5], Turkey [6], and Chile [7, 8]. Boron can be found as a native component of soils and can also be introduced with irrigation water. A particularly important source of excess B to agriculture is found when recycled wastewater is used for irrigation [9]. In spite of the extent of excess B in the arid zones, research and knowledge concerning B toxicity is less than that of B deficiency.

Boron in soils and agricultural systems has been widely reviewed in the past. Keren and Bingham [2] and Goldberg [1] thoroughly discussed B chemistry and B-soil interactions, Gupta et al. [10], offered a comprehensive look at B in plants, Nable et al. [11], Stangoulis

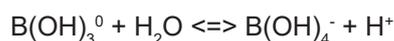
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and Reid [12] and Yau and Ryan [13] specifically dealt with B toxicity, as did Reid et al. [13] and [14] in physiologically based discussions. Readers wishing in-depth treatment of these topics are encouraged to turn to those sources.

This review aims to focus on B interactions with soils and plants in arid and semi-arid regions. A basic introduction to B in soils and solutions and to B in the soil-water-plant continuum is provided here to give the reader sufficient background to understand the issues of B in arid-zone agriculture. Commonly, excess B in arid regions is accompanied by conditions of high salinity [2]. These topics are reviewed in terms of their relevance to arid agriculture and are discussed using case studies from Israel's Negev desert region.

2. Boron chemistry

The coordination number of the B minerals is either 3 or 4 or a combination thereof. In solution, $B(OH)_3^0$ behaves as a very weak Lewis acid ($K_a = 6 \times 10^{-10}$, pK_a 9.1) according to the equilibrium equation:



At low concentration (≤ 0.2 mg/l), only the mononuclear species $B(OH)_3^0$ and $B(OH)_4^-$ are present. At higher concentrations and with increasing pH, polynuclear ions, such as $B_2O(OH)_6^{2-}$ or those incorporating B_3O_3 rings, are formed. Further increase in pH results in higher nuclearity borates, but above pH 10, $B(OH)_4^-$ is produced exclusively [15]. Complexation with B is mostly limited to compounds having two hydroxyl groups in the *cis*-conformation, classified as *cis*-diols. The most stable of these complexes are formed with *cis*-diols attached to a furanoid ring [16]. In this way B binds to plant sugars, soil organic matter, metal oxides and clays.

3. Boron soil interactions

Boron transport in soils and B available for plant uptake is a function of B concentration in the soil solution. B in soil solution is determined by: a) soluble B entering the soil-water system; either from the soil mineral fraction or from B imported through groundwater or irrigation water; and b) sorption reactions between the aqueous soil solution and soil solids.

3.1. Sources of soil B

Boron is widely distributed [17] in both the lithosphere and hydrosphere. In rocks its concentration averages about 10–20 mg B/kg. In sea water it can range from 1–10 mg B/l, while its concentration in fresh surface waters is generally much lower. A survey of 1542 surface water samples reported a mean B concentration of 0.1 mg/l [18]. However, concentrations up to 1000 mg/l have been measured in salt lakes and hydrothermal waters [19]. Most soils have low B content (less

than 10 mg/kg); high B content soils are those associated with recent volcanism [15] and arid or semi-arid regions. Groundwater can be high in B if exposed to geological formations with soluble B. Boron-containing minerals are either insoluble (tourmaline) or very soluble (hydrated B minerals).

3.2. Soil solution B – adsorption processes

The relative solubility of minerals generally is not found to control the concentration of B in soil solution [1]. The B concentration in the soil solution is instead much more highly influenced by B adsorption reactions. The amount of B adsorbed by soils varies greatly with the contents of soil constituents, the most important being clay minerals, sesquioxides and organic matter [2]. Calcium carbonate acts as an important B adsorbing surface in calcareous soils. Boron adsorption is greater in soils having higher calcium carbonate content [20]. The mechanism of B adsorption is generally considered to be ligand exchange. On a per-weight basis, clay minerals adsorb significantly less B than do most oxide minerals and organic matter.

Layer-silicate clay minerals adsorb B; the order of B adsorption on a per-weight basis is kaolinite < montmorillonite < illite [21]. The rate of B adsorption to clay minerals begins with an initial, fast adsorption reaction (less than one day) followed by a slow diffusion of B into the crystal lattice [22]. Initially, B adsorbs to the surface hydroxyl groups on the clay particle edges. Subsequently the B migrates and is incorporated structurally into tetrahedral sites, where it replaces structural silicon and aluminium.

Boron adsorbs on both crystalline and amorphous aluminium- and iron-oxides. Boron adsorption is greatest on freshly precipitated solids, decreases with aging due to increasing crystallinity [23], and is greater for aluminium oxides than iron oxides [24] on a per-weight basis. Magnesium (Mg) hydroxide can remove appreciable amounts of B from solution. Due to Mg hydroxide coatings, silicate minerals containing mainly Mg in their chemical formulas adsorb more B than silicate without Mg. The appreciable B adsorption capacity of the sand and silt fractions of arid zone soils low in clays and organic matter may therefore result from clusters and coatings of Mg hydroxide on silicate minerals [25].

Knowledge concerning B adsorption to organic materials is much less comprehensive than that concerning clays and metal oxides. It is nevertheless understood that soil organic matter significantly affects B distribution between the soil's solid and liquid phases and influences B uptake by plants. Boron adsorbs on all soil organic matter constituents [26, 27], including natural organic matter like compost and peat [28, 29]. Garate and Meyer [30] concluded that the main factors affecting B retention by organic matter were pH, Ca and fulvic acid content, and the humic-to-fulvic

acid ratio. Interaction between B and organic matter can alter soil solution B. Boron deficiency has been observed in soils with high organic matter content [31-34]. This deficiency has been shown to be related to the high affinity of organic matter to B [28, 33, 35, 36] and its removal from solution. In a case where a small amount of composted organic matter not rich with B was added to the soil (Loess, Calcic Haploxeralf) the number of adsorption sites was significantly increased and soil solution B and plant uptake were decreased [37]. Alternatively, adding organic matter to soil has been reported to increase B content and its availability to plants [38, 39].

Factors influencing B adsorption and desorption from soil constituents include: B concentration in the soil solution, solution pH, presence and type of exchangeable ions, ionic composition of the soil solution, wetting and drying cycles and temperature [1, 2]. Boron adsorption on soils is particularly dependant on solution pH. Boron adsorption on soil constituents increases with increasing pH, reaches maximum levels at around pH 9 and decreases with further increases of pH [40]. The pH dependence of B adsorption can be explained by competition between borate ions, boric acid and hydroxyl ions for specific sorption sites [21]. Quantitative relationships between solution concentrations of the ions are a function of pH but not by adsorption characteristic or number of adsorption sites [21, 28].

Information concerning the reversibility of B adsorption reactions in soils is contradictory. For some soils, desorption isotherms correspond closely to B adsorption isotherms while other soils exhibit hysteresis [20]. In investigations of the cause of hysteresis, no significant correlation was found with soil properties including: clay, organic carbon, pH, electrical conductivity (EC), cation exchange capacity, surface area, aluminum oxide content, or iron oxide content [20]. Mechanisms of irreversibility of B sorption have been shown to include: ligand exchange, formation of bidentate surface complexes and incorporation of B into clay mineral lattices [1].

Boron adsorption and desorption from soil adsorption sites regulate B concentration in the soil solution. This regulation itself is a function of the changes in solution B concentration and of the affinity of the soil constituents for B [41]. Thus, adsorption of B may buffer fluctuations in solution B concentration such that B concentrations in soil solution may vary only slightly with changes in soil water content.

3.3. Leaching B from soils

Soluble salts, including B, existing in the soil can be moved out of the root zone with water applied for this purpose. Boron as boric acid or borate is mobile in soil solution. The capacity for leaching B from the root zone is a function of water content and water movement in

the soil as well as of B transport processes (which are themselves affected by B adsorption-desorption processes). In general, the amount of water needed to leach B from soil is much higher than that needed to remove non-reactive solutes like Cl^- or Br^- .

A column study [42] showed that the amount of water, measured in terms of pore volumes, to achieve transport of B so that adsorption and desorption processes reached equilibrium and maximum B moved out of the soil was 4–8 times greater for B transport compared to the ideal mass-transfer of Br^- . Actual transport and leaching of B, however, are determined by the same parameters that affect the B adsorption-desorption process. For example, transport of B through soil columns was retarded by increased clay content and by increased solution pH [42].

Boron transport in a loamy sand soil was also strongly controlled by rate-limited adsorption, which, in turn, was dependent on pore-water velocity [43]. Information from B adsorption-desorption processes studied under equilibrium conditions (as in the column experiments) can and are used to predict B transport in soil [44, 45], but the assumption of equilibrium may not be appropriate for actual field conditions, where the parameters and processes controlling B movement would likely vary with space and time. Communar and Keren [43] found rates of B adsorption that were higher than those of B desorption in non-equilibrium conditions. The pH in soil solution, well established as having primary importance to adsorption processes, often varies as a function of time, location in the field and soil depth [46]. Shouse et al. [47] monitored salinity and B concentration in a 60-ha agricultural field. Soil salinity and B concentrations were found to be highly correlated and were observed to be largely a product of soil textural variations. A number of additional factors, such as water redistribution and solute concentration augmentation by evaporation, can also affect B transport in unsaturated soils under transient water flow regimes [48]. Increases in solution B concentration caused by evaporation are compensated, in part, by B adsorption, whose effect depends on the rate of adsorption-desorption reactions.

The maximum effect is achieved when adsorption occurs instantaneously (equilibrium adsorption). Under rate-limited adsorption, the concentration of B in the solution changes; it parallels the variation of water content, with some time lag. Communar and Keren [48] estimated the effect of transient, non-monotonic water flow on B transport in unsaturated, homogeneous loamy sand and loess soils. Their results indicate that non-steady-state conditions caused by interruptions in flow affect B transport and lead to significant changes in solution B. In spite of this, lysimeter studies investigating the effect of excess B in irrigation water on crops suggest that in regularly irrigated

soils assumptions of B-adsorption equilibrium may in fact be reasonable, as long as concentration of B in applied water stays constant. Full-season studies on tomatoes in a sandy loam soil indicated that drainage water B reached steady-state values after 20–50 days of irrigation and that the time to steady-state increased with increased irrigation water B concentration and decreased with increased irrigation volumes [49].

A long-term experiment with date palms grown in lysimeters and irrigated with B-salinity combinations [50, 51] also showed that in the sandy loam soil studied, in a very hot dry climate, a leaching fraction of 0.25 was sufficient to provide equilibrium conditions for B in 1 m³ containers after 3–5 months and that steady-state conditions of B in soil solution and in drainage water were maintained for years thereafter.

4. Boron in plants

4.1. Plant function and B nutrition

Boron plays an apparent role in a number of physiological processes in plants, including: cell enlargement and division in roots and leaves, microsporogenesis and pollen tube growth [52], sugar transport, cell wall synthesis, lignifications, cell wall structure, carbohydrate metabolism, RNA metabolism, respiration, indole acetic acid (IAA) metabolism, phenol metabolism, membrane integrity, and ascorbate metabolism and induce oxygen activation [53-55]. Hu and Brown [56] discuss B deficiency in detail and suggest that “the rapid and specific inhibition of plant growth that occurs upon removal of B is a consequence of two important features of B physiology: the specific structural role B plays in the cell wall and the limited mobility of B in the majority of species”.

Boron uptake in higher plants occurs passively through the lipid bilayers and is a function of external boric acid concentration, membrane permeability, internal complex formation and transpiration rates [56]. Aquaporins in plants can also transport small neutral solutes [57, 58] and that passive lipid diffusion and aquaporins or other Hg-sensitive channels [59-61] serve as possible pathways of B into the plant.

Boron is mobile in the xylem and its transport within the plant is primarily via mass flow with the transpiration stream. Beyond the xylem, B is generally considered highly non-mobile in most plants, as it accumulates in leaves and is normally not found to be transported to other organs or locations. Only in particular plant species that produce polyols that complex with the B and allow its transport has B been demonstrated to be mobile in the phloem [62]. Molecular, genetic and physiological studies show that B transport in plants not only occurs by passive diffusion across membranes but is also catalyzed by regulated transport proteins (NIPs (nodulin-26-like intrinsic proteins), boric acid channels,

and BORs, B exporters). These transporters function to support normal growth under high B conditions [63].

4.2. Excess B and toxicity

High B concentrations in soil solution leads to plant toxicity. The range of B concentrations in the soil solution causing neither deficiency nor toxicity symptoms in plants is particularly narrow [2]. For a wide variety of plant species, the primary visible symptoms of B toxicity are chlorotic and/or necrotic patches that first appear at the margins and tips of mature leaves. These symptoms are typical in most plants, where, as previously mentioned, B mobility is restricted to the transpiration stream and excess B accumulates in leaves [11]. The extent of B toxicity symptoms is a function of B accumulation in the leaves which, in turn, depends on the B concentration in soil solution, length of exposure, transpiration rate and species and genotype. Root elongation can be decreased by high B [64] but the concentration in soil solution causing such a response is much higher than that leading to visual symptoms of toxicity in shoots since B concentration in the roots remains relatively low compared to that in leaves. Contrary to most species where B is immobile, in species in which B is phloem mobile the symptoms of toxicity are flower and fruit disorders, bark necrosis which appears to be due to death of cambial tissues, and stem die back [65]. Recently, Reid [66] concluded that B movement in plants involves is of a complex multi-layered system designed to optimizing the use of B utilization over a broad range of concentrations. At the cellular level, plants can switch the direction of B flow through the polar expression of membrane transporters, while at the whole plant level, integration of xylem and phloem transfer can deliver B to specific tissues dependent on developmental stage.

Plant response to exposure to high B has long been understood to be species specific [67]. In a number of crops, there is also a wide range of genotype- or variety-specific variation in response to excess B [68]. Boron toxicity is also a function of type of exposure; the relative toxicity of B entering through the leaves when foliage is exposed to B-laden water is greater than that of B entering via roots [69]. We do not yet sufficiently understand the mechanisms for B toxicity in sensitive plants or how tolerant plants evade toxicity [14, 64, 70]. Sensitivity to B is accompanied by significant changes in the physiology and activity of numerous enzymes and apparently involves a number of metabolic processes, including reduced expansion in meristematic regions, development of necrotic areas in mature tissues (reduced photosynthetic capacity), reduced supply of photosynthate to developing regions of the plant, and, at particularly high B levels, inhibited root growth. Toxicity may be associated with the form of B in plants and that soluble B holds greater importance than total B [70-72].

4.3. Drought and B toxicity

Stress due to low moisture levels is common in arid regions. Adsorbed B was found to be independent of variations in soil moisture content from 50 to 100% of field capacity in one study [73] and increased with decreasing soil water content in another [41]. Wetting and drying cycles increased the amount of B fixation [74] with the effect of drying becoming more pronounced with increased additions of B. Boron availability has been alternatively reported to decrease or increase as soils dry [1]. The differences may be due to expected effects of drying on root distribution and activity in regards to B in the soil profile. Fleming [75] found B deficiency in plants in dry soils because the lower depths where roots extracted water when the upper profile was depleted contained little B. Yau [76], on the other hand, reported increased B uptake under drought conditions, as the deeper soil in his study was particularly high in B. Little is known concerning interactive effects of boron toxicity with water stress on plants [49, 76]. Shani and Hanks [77] modeled B toxicity, salinity and drought stress based on independent multiplicative factors but their range of experimental crops and stress factor levels was limited.

Ben-Gal and Shani [49] tested five irrigation levels (30, 60, 100, 130 and 160% of potential evapotranspiration) with three B-water concentrations (0.3, 4.0 and 8.0 mg/l) on tomato transpiration and biomass production. They found that low moisture levels and high B in some cases led to higher leaf B content, but never to lower yield, and concluded that simultaneous B and drought stresses did not result in greater toxicity but, rather, one or the other stress-causing factor was found to be dominant in plant response. Yau [76], alternatively, reported that drought conditions led to increased B accumulation and increased B toxicity effects in barley growth. The expression of more severe B toxicity when water is limiting was explained by the tendency of drought-affected plants to grow roots deep into the subsoil where B had accumulated. Contrary to this result, Hamurcu et al., [78], who investigated the effect of different B treatments on drought tolerance of watermelon plants, showed that increasing dosage of B alone caused more severe growth reduction than when combined with PEG 6000-induced drought stress. Drought stress caused less accumulation of B in leaves and roots. They also showed that high B caused lipid peroxidation in a reactive oxygen species-independent manner and drought stress-induced lipid peroxidation was alleviated by increasing B dosage.

5. Boron-salinity interactions

Soils in semi-arid and arid regions where little or no leaching occurs tend to have high levels of B, but also are high in overall salinity [2]. In these regions, water available for irrigating agricultural crops can also contain high concentrations of salts along with B [11]. Crops in such areas are therefore prone to simultaneous exposure to stress-causing factors from both

salinity and excess B. Examples of native soils with naturally high levels of salt and B are found in the Jordan Valley, shared by Israel and Jordan, and in soils of South Australia, where underlying shallow, saline-high B water tables can be prevalent [79]. Irrigation with saline groundwater containing high B concentrations occurs in many dry regions with notable examples found in California's San Joaquin Valley [80], Texas's Rio Grande Valley [81] Canada's Saskatchewan Province [82], in Israel's Negev region [5], and in Chile's Lluta Valley [8]. An additional source of combined high levels of salts and B is found in recycled wastewater [9, 83], which is increasingly used water source for irrigation.

5.1. Boron-salinity interaction in soil

Salinity can influence B-soil interactions both directly, by affecting sorption processes, and indirectly, by altering the soil's hydraulic conductivity, thereby affecting B transport and leaching. Boron adsorption on clays increases with the increasing ionic strength of the solution [22, 28, 84]. The influence of ionic strength was found to be greater for sodium clays, as compared to calcium clays [84]. Increasing ionic strength with CaCl_2 increases B adsorption on organic matter, as well [28]. Increasing ionic strength enhances the dissociation of boric acid in solution to higher affinity borate ions [85], thus increasing B adsorption. Additionally, increased ionic strength of solution diminishes the width of double-diffused layers, enabling greater concentration of borate adjacent to mineral surfaces and increasing B adsorption even more [2]. The presence of chloride, nitrate or sulfate has little effect on B adsorption on clays, while the presence of phosphate appreciably reduces B adsorption [1].

High sodium concentrations can lead to clay dispersion, loss of soil structure and porosity, and subsequent reductions in soil hydraulic conductivity. Leaching of B in sodic soils is therefore particularly difficult, as water movement through the soil indirectly decreases the mobility and transport of B.

5.2. Boron-salinity interaction in plants

Plant stresses caused by salinity or B alone have been thoroughly investigated and, while their independent effects on growth and yield have been well described in the literature [10, 11, 86, 87], less knowledge exists concerning cases where they occur concurrently. Bingham et al. [88] found that the shoot weight of wheat was not affected by interaction between B concentration (in the range of 0.09 to 1.39 mM) and salinity (in the EC range of 0.5 to 4.2 dS/m). A similar conclusion was reached by Mikkelsen et al. [89] for alfalfa plants and by Grattan et al. [90] for eucalyptus. Shani and Hanks [77] grew barley and corn in the field and concluded that the osmotic and B effects were additive rather than interdependent. Ferreyra et al. [7] observed that the growth of 42 different kinds of plants was higher than expected from the sum of the

two factors, a finding that indicates amelioration of B toxicity by salinity. Holloway and Alston [91] and Grieve and Poss [92] showed that the response of wheat to B decreased with increasing salinity. Similar trends were found for tomato [93, 94], chickpea [95], grapevines [96], and date palm [51].

The nature of the interaction of combined B and salinity effects can be additive, antagonistic or synergistic. Data for bell pepper [97] and reanalysis of data from the literature for wheat [88] and tomato [94] imply amelioration of toxicity (an antagonistic relationship) regarding growth and yield for combined B toxicity and salinity [97]. Antagonism between salinity and B may be a result of decreased toxicity of B in the presence of NaCl, reduced toxicity of NaCl in the presence of B, or both together. Yermiyahu et al. [97] suggested a possible explanation for bell peppers, where uptake of B is reduced in the presence of Cl and uptake of Cl is reduced in the presence of B. Masood et al. [98], grew wheat hydroponically and found that Cl was reduced in plants by excess application of B. At adequate B supply, NaCl increased apoplastic and symplastic soluble B concentrations, whereas the total B content remained unchanged. At a high B level, however, soluble and total B were reduced by salt stress. They concluded an alleviating effect of the combined stresses on toxic ion concentrations, which did not prevent additive growth reductions. However, the mechanism of B-salinity interactions is not clear and there are currently no satisfactory physiological or physical explanations for B-Cl uptake interactions.

Wimmer and Goldbach [99] studied five different B and salt-resistant wheat genotypes grown hydroponically with low and high B supply. Boron-uptake rates were reduced with increasing salt concentration only under high B supply. They suggested that under high B supply, when B uptake is predominantly passive by diffusion or channel-mediated via aquaporins, transpi-

ration-driven water flow is the dominant factor for B accumulation in aerial plant parts. Under low B supply, when a significant portion of B can be taken up via active pathways, transpiration is not the decisive factor for B accumulation. Bastías et al. [100] investigated the effect of B compared to Ca in order to elucidate whether the two nutrients have similar effects and/or to reveal a relationship under salinity. They showed increase of aquaporin functionality under the presence of both B and Ca compared with NaCl-treated plants. del Carmen Rodríguez-Hernández [101] studied water transport and membrane integrity of broccoli (*Brassica oleracea* L.) in response to B and salinity. Their results suggest that B and NaCl trigger a hydric response involving aquaporins, together with changes in nutrient transport and plasma membrane stability. Research on broccoli at the USDA-ARS U.S. Salinity Laboratory showed complex interactions between salinity, B, and pH [102-105].

6. Bioavailability and toxicity of residual B in managed soils in irrigated dry-zone agriculture

6.1. Case study 1 – natural soil B in vineyards in the Jordan Valley

Orchards and vineyards dominate the landscape in Israel's Jordan Valley where the hot, dry climate contributes to the potential for early-season fruit production. The native soils in the Jordan Valley are in many cases saline [106] and are prone to high levels of B. B toxicity has been hypothesized as an explanation for chlorotic leaf edges observed during vegetative growth periods, particularly late in the season, in table grape vine production in the Jordan Valley (Fig. 1). Grape production in the Jordan Valley had steadily declined and average fruit size decreased. In addition, the lifespan of vineyards in the region was found to be substantially reduced compared to other regions growing the same varieties (Pini Sarig, personal observation).

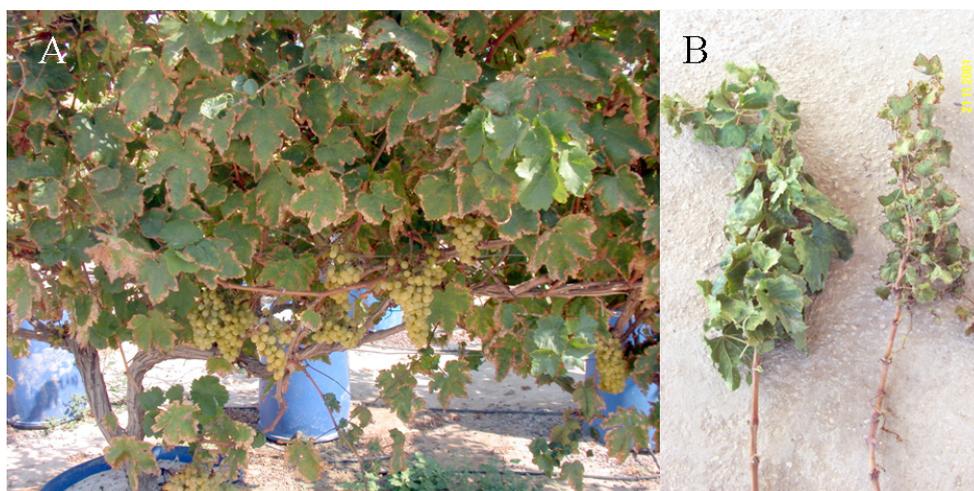


Figure 1. Boron toxicity symptoms on grapevines (Sugarone on Ruggeri) grown in containers in the Jordan Valley, Israel: (A) symptoms on leaves of vine irrigated with water containing 3.1 mg/l B; (B) branch from grapevine irrigated with low-boron (0.3 mg/l, left) and high-boron (3.1 mg/l, right) solutions (from Yermiyahu et al. [107]).

A study was carried out to investigate the leaching of salts and B from soils in Jordan Valley commercial vineyards and to evaluate the effects of residual B on grapevines. This study revealed cases of long-term B toxicity even after leaching and when good quality-low B water was used for irrigation. Three- to six-year-old plots planted with three varieties of table grapes on Ruggeri rootstock (Table 1) were chosen in commercial vineyards where non-cultivated soil adjacent to the plots could be compared to the cultivated soil in the vineyard. Soils in the vineyards were alluvial,

with dominant textures ranging from loam to clay. Sites 3 and 4 had an upper horizon up to 30-cm thick that was sandy loam and lower horizons with up to 30% clay. Sites 1 and 2 had higher clay levels throughout the profile, with up to 50% clay. Vineyards were drip-irrigated with local water with EC = 0.9 dS/m and B = 0.05 mg/l since the vines were planted. Sampling pits were dug using a back hoe in March of 1999.

Three pits were dug at each site; two inside the vineyard adjacent to vine rows and a third outside of the

Table 1. Description of vineyard plots sampled for soil B and salinity levels and monitored for B toxicity; "low", "medium" and "high" B levels reflect visual evaluation of toxicity symptoms on grapevines.

Plot no.	Location	Variety	Age (years)	Boron toxicity level
1	Tomer	Perlet	5	low
2	Gilgal	Perlet	3	low
3	Yitav	Sugarone	6	medium
4	Nativ Hagdud	125	6	high

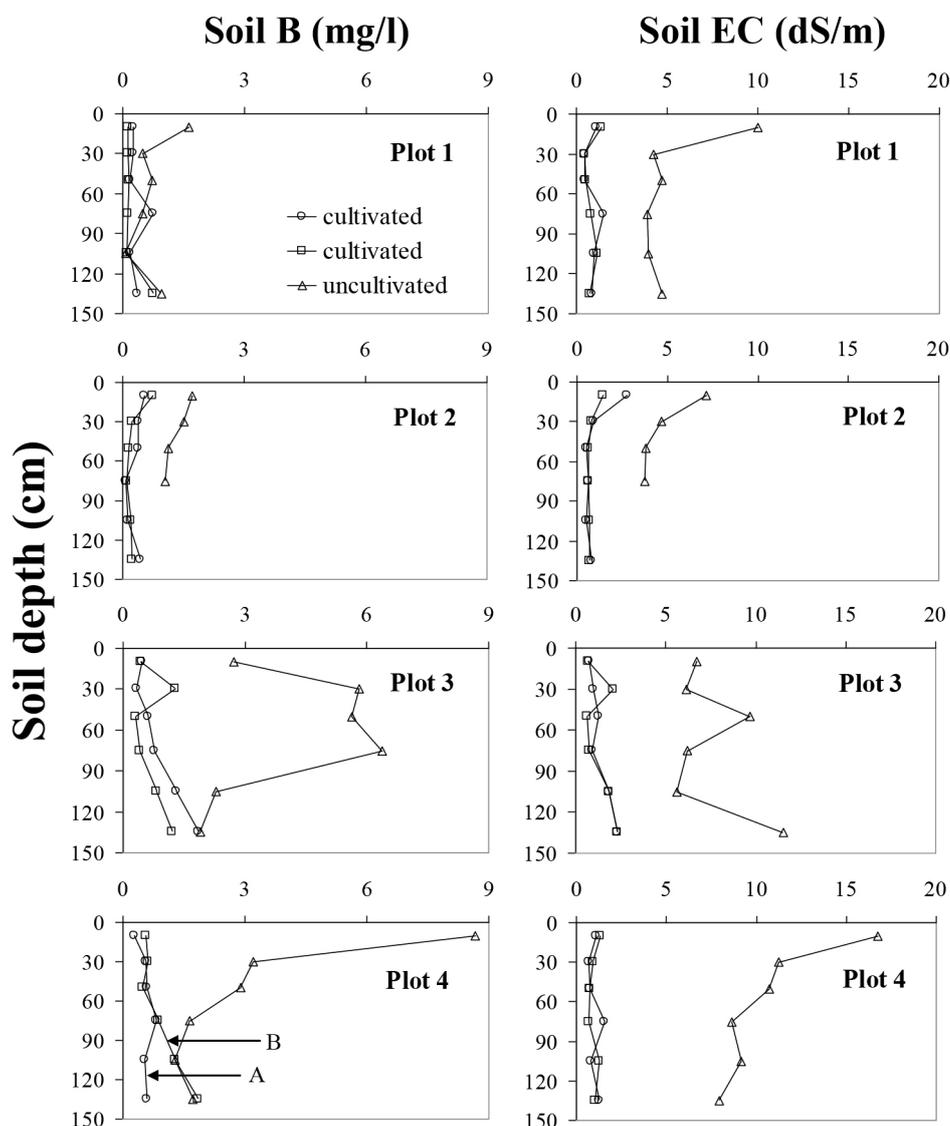


Figure 2. Saturated paste B and EC as a function of depth in four vineyards in the Jordan Valley; samples were taken at the onset of the growing season from three locations in each plot: two adjacent to vine rows and one outside the cultivated area.

cultivated area. Soil was sampled from the pits 50 cm from the drip line at 0–20, 20–40, 40–60, 60–90, 90–120 and 120–150 cm depths from the surface and used to determine saturated paste EC (EC_e) and B (Be). Samples of diagnostic leaves from grapevines were taken on two dates in each of three years: after flowering (second or third week of March – leaves growing adjacent to flowering clusters), and at the end of the season (second or third week of November – the most mature young leaf to the fifth leaf from the end of branch). Three replicates were sampled for each plot, 40 leaves per sample.

The EC_e and Be in the uncultivated soil reached 17 dS/m and 9 mg/l in saturated paste extracts, respectively (Fig. 2 plot 8). In cultivated soil, salinity and B significantly decreased, with EC_e as low as 1.2 dS/m and Be as low as 0.4 mg/l. This depletion followed pre-planting leaching and continual-leaching irrigation regimes during growing seasons. The EC_e in the soil profile of all the plots was consistently lower than 2 dS/m, which is considered to be a critical value for grapevine response [108], below which yield is not reduced.

Boron in the sampled Jordan Valley soils was highly variable (Fig. 2). In the data presented, two of the plots were high in B while two had much lower B levels. In both sets of soils the B in the uncultivated pits decreased with depth and in cultivated soil B increased with depth. In the low soil-B content plots, B concentration ranged from 0.1–0.3 mg/l, while in the high soil-B content plots, B concentration was more than five-fold higher. The ratio of B in cultivated to B in uncultivated soil was greater as depth of sampling increased. At 150 cm below the surface the B concentration in cultivated plots, where natural B levels were high, was more than 2 mg/l, a level of B that is considered toxic and has been found to induce toxicity symptoms in grapevines [107, 108].

Analysis of leaf samples confirmed that B uptake and accumulation was greater in plots where B was originally higher and where deep soil contained relatively high residual B (Fig. 3). Boron accumulated in leaves throughout the growing season. Samples taken at the beginning of the season had lower B content: 100 and 160 mg/kg for plots 1 and 4, respectively. Boron in leaf material collected at the ends of the seasons reached 900 mg/kg in vines grown in the higher-B soil (Plot 4) while B levels in leaves from vines grown in soils with lower B were ~300 mg/kg (plots 1 and 2).

Roots were observed in the sampling pits in the entire profile up to 200-cm depth. Root activity at the greater depths, where B is relatively high, would explain observations of B toxicity symptoms in these soils, even when B in the upper horizons was low. For example, the profile in Fig. 2, labeled (A), was taken adjacent to a healthy vine while that labeled (B) was located close to a vine that exhibited B toxicity symptoms. The soil B in the first profile was <1.0 mg/l at all depths. The

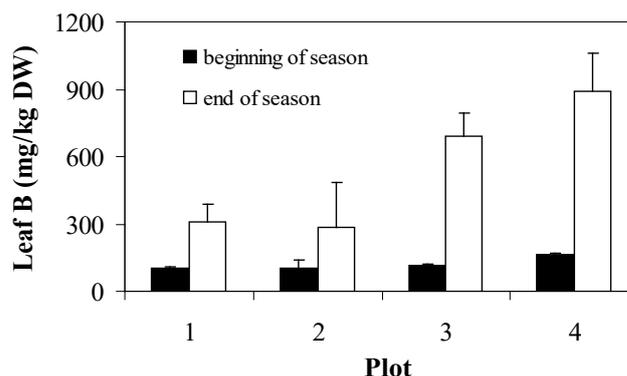


Figure 3. Concentration of B in diagnostic leaves from grapevines sampled early in and near the end of three growing seasons; columns show average values and lines represent standard deviations for the three sampling seasons; plots 1 and 2 had correspondingly low soil B, while plots 3 and 4 had correspondingly high soil B.

soil B in the second profile was very similar to the soil B in the first profile down to 60–90 cm, but at greater depths it increased significantly to 1.5 mg/l in saturated paste extract. Apparently, root uptake of water at the greater depths led to B uptake and subsequent accumulation and toxicity. One solution to this problem would be to further leach the B to even greater depths. A second possible solution would be to change current agronomic practices in the region, where irrigation is reduced following harvest, and stopped completely in the winter while the vines are dormant. Such management (no winter irrigation) encourages root expansion and activity into deep soil where the B concentrations can be high. Alternative management, where irrigation is continued to maintain relatively high soil moisture in the upper leached horizons all year long, would likely resolve the problems of B toxicity.

6.2. Case Study 2 - B originating from saline irrigation water in Israel's Western Negev

For a period of over 20 years, beginning in the 1970s, low-quality irrigation water, characterized by high levels of sodium salts, an EC of 3–5.5 dS/m and B concentrations reaching 2.0–3.5 mg/l was utilized to irrigate cotton in Israel's Western Negev region. Management routinely involved pre-plant winter application of gypsum to the area's loess soils to offset sodicity problems and to facilitate infiltration, followed by summer cotton cultivation. Recently, as profits from cotton cultivation have declined, the practice of irrigating with saline water has been discontinued and cotton has been replaced by less salt-tolerant crops including peanuts and potatoes. In cases where peanuts were cultivated on fields that had previously supported cotton irrigated with the saline water, phenomena including leaf desiccation and reduced growth and yields of nut pods were observed.

To investigate the problems in peanut cultivation, adjacent fields at Kibbutz Nir Oz with and without histories of irrigation with saline water were selected. Water quality parameters for the saline water, for

fresh water used for irrigation until 1989, and for high-quality tertiary treated municipal wastewater (Shafdan) used henceforth are given in Table 2. Peanuts planted in June 2003 in 10 plots in each field were monitored. The winter rainfall and the amount and type of irrigation water applied from 1980 to 2002 are presented in Table 3. Soil physical characteristics

(Table 4), including texture and hydraulic properties, were uniform throughout the plots. Soil was sampled at the beginning and end of each cropping season and ECe and Be were determined as a function of depth to 120 cm. Leaf samples from peanut plants were taken five times during the growing periods and tested for accumulated salts and

Table 2. Average values of some quality parameters for the three water sources historically used to irrigate Kibbutz Nir Oz fields: Fresh, saline, and treated waste water (Shafdan)

Characteristic	Water type		
	Fresh	Saline	Shafdan
Electrical Conductivity (dS/m)	1.1	4.2	1.3
Chloride (meq/l)	7.1	31.0	6.9
Sodium (meq/l)	4.6	40.0	5.8
Calcium + Magnesium (meq/l)	5.0	6.0	6.4
Boron (meq/l)	0.2	2.1	0.3
Sodium Adsorption Ratio	2.9	23.0	3.2
pH	7.3	7.5	7.6

Table 3. Crop growth and irrigation history of fields watered with saline (contaminated) and fresh water (uncontaminated).

Year	Rain fall (mm)	Contaminated field			Uncontaminated field		
		Crop	Water	Amount (mm)	Crop	Water	Amount (mm)
1980	360	cotton	saline	500	wheat	-	-
1981	235	cotton	saline	470	wheat	-	-
1982	235	cotton	saline	510	peanut	fresh	700
1983	387	cotton	saline	520	potato	fresh	475
1984	144	cotton	saline	480	wheat	-	-
1985	205	cotton	saline	485	wheat	-	-
1986	226	cotton	saline	490	peanut	fresh	700
1987	326	cotton	saline	517	potato	fresh	475
1988	298	cotton	saline	520	wheat	-	-
1989	348	cotton	saline	510	wheat	-	-
1990	276	cotton	saline	540	peanut	Shafdan	700
1991	286	cotton	saline	540	potato	Shafdan	475
1992	427	cotton	saline	550	wheat	-	-
1993	304	cotton	saline	520	wheat	-	-
1994	141	-	-	-	wheat	-	-
1995	452	cotton	saline	530	peanut	Shafdan	700
1996	217	cotton	saline	540	potato	Shafdan	475
1997	282	-	-	-	wheat	-	-
1998	251	wheat	saline	80	wheat	-	-
1999	64	-	-	-	peanut	Shafdan	700
2000	177	wheat	saline	80	potato	Shafdan	475
2001	287	potato	Shafdan	420	wheat	-	-
2002	251	wheat	-	-	wheat	-	-
Total	6179			8802			5875

Soil salinity was similar at the beginning of the seasons in the plots with a history of saline irrigation and in those without such a history down to a depth of 90 cm (Fig. 4). Deeper samples revealed higher salinity ($EC_e = 5$ dS/m) in fields with a history of saline irrigation than in those without such a history ($EC_e = 2$ dS/m). At the end of the growing seasons, these differences were reduced (Fig. 4). Boron concentration along the profile in soils with a history of saline irrigation ranged from 1.2 to 2.0 mg/l (Be), substantially higher than the B concentration in the soils with no history of saline irrigation, which ranged from 0.3 to 0.5 mg/l.

At the end of the season, slightly greater Cl and Na were found in plants grown in plots with a history of saline irrigation (Table 5). Boron content of plant leaf matter in the plots with a history of saline irrigation was significantly greater as it reached 150–250 mg/kg dry matter compared to 50–90 mg/kg dry matter for plants in the plots with no such a history. Vegetative biomass production was 21% lower for plots with a history of saline irrigation as compared to the other plots. Pod yield for peanuts was 38% lower in the plots with a history of saline irrigation (Table 5).

Table 4. Representative values of parameters for soils at Kibbutz Nir Oz, Israel.

Soil depth (cm)	Texture (%)			Lime (%)	Cation Exchange Capacity (meq/100g)
	Clay	Silt	Sand		
0-30	15.0	5.0	80.0	8.5	6.9
30-60	17.5	10.0	72.5	11.0	7.7
60-90	22.5	10.0	67.5	16.2	9.9
90-120	20.0	17.5	62.5	25.3	8.4

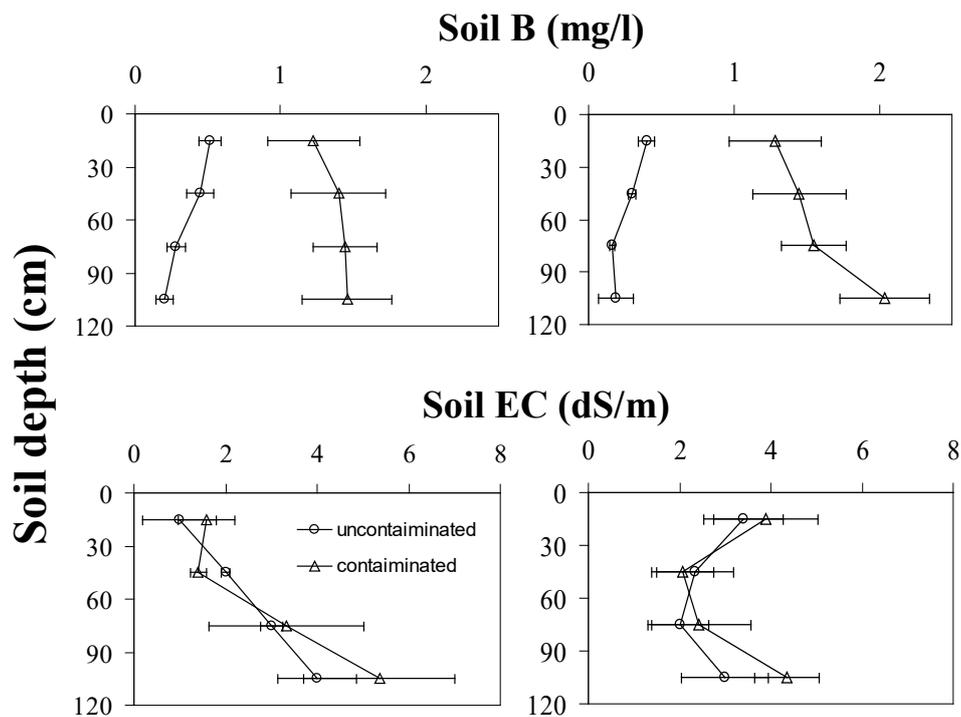


Figure 4. Boron concentration and electrical conductivity (EC) in saturated paste from soil sampled at the beginning (left) and the end (right) of a growing season.

Table 5. Mineral content in leaves and peanut yield in uncontaminated and contaminated fields.

	Uncontaminated field	Contaminated field
Boron (mg/kg)	50-90	200-250
Chloride (%)	0.73-1.70	0.65-2.05
Sodium (%)	0.09-0.13	0.12-0.22
Dry matter (g/plant)	66.6	51.2
Pod yield (ton/h)	44.3	27.6

Long-term irrigation with low quality (high salinity, high B) water was found to have lasting effects on soil chemistry and crop production, due to the residual B in the soils. After switching to high-quality water, excess irrigation and winter rains caused sodium chloride to be leached out of the root zone. Boron, on the other hand, adsorbed to soil components (clays and organic matter) and remained in the soil at rather high levels. This B clearly remained available for plant uptake, and led to reduced yields in the peanut crop.

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7. References

- [1] Goldberg S., Reaction of boron with soil, *Plant Soil.*, 193, 35-48 1997.
- [2] Keren R., Bingham F. T., Boron in water, soils and plant, In: *Advances in Soil Science*, (R. Stuart, ed), Springer-Verlag, New York, 1, 229-276, 1985.
- [3] Cartwright B., Zarcinas B. A., Spouncer L. R., Boron toxicity in South Australian barley crops, *Aus. J. Agric. Res.* 37, 351-359, 1986.
- [4] Banuelos G. S., Cardon G. E., Phene C. J., Wu L., Akohoue S., Zambruski S., Soil boron and selenium removal by three plant species, *Plant Soil* 148, 253-263, 1993.
- [5] Yermiyahu U., Zilberman J., Ben-Gal A., Keren R., Bioavailability and toxicity of residual boron originating from saline irrigation water, *World Congress of Soil Science*, Philadelphia, USA, July 10-15, 2006.
- [6] Torun B. M., Kalayci L., Ozturk A., Torun M. A., Cakmak I., Differences in shoot boron concentrations, leaf symptoms, and yield of Turkish barley cultivars grown on boron-toxic soil in field, *J. Plant Nutr.*, 26, 1735-1747, 2002.
- [7] Ferreyra R. E., Aljaro A. U., Ruiz R. S., Rojas L. P., Oster J. D., Behavior of 42 crop species grown in saline soils with high boron concentrations, *Agric. Water Manag.*, 34, 111-124, 1997.
- [8] Bastías E. I., González-Moro M. B., González-Murua C., Zea mays L. amyloacea from the Lluta Valley (Arica-Chile) tolerates salinity stress when high levels of boron are available, *Plant Soil.*, 267, 73-8, 2004.
- [9] Tsadilas C. D., Soil contamination with boron due to irrigation with treated municipal waste water, In *Boron in Soils and Plants*. Eds R. W. Bell and B. Rerkasem, Kluwer Academic Publishers, Dordrecht, 265-270. 1997.
- [10] Gupta U. C., James Y. W., Cambell C. A., Leyshon A. J., Nicholaichuk W., Boron toxicity and deficiency: A review, *Can. J. Soil Sci.*, 65, 381-409, 1985.
- [11] Nable R. O., Banuelos G. S., Paull J. G., Boron toxicity, *Plant Soil.*, 198, 181-198, 1997.
- [12] Stangoulis J. C. R., Reid R. J., Boron toxicity in plant and animals, In: *Boron in Plant and Animal Nutrition* (H.E. Goldbach, B. Rerkasem, M.A. Wimmer, P.H. Brown and R.W. Bell, eds), Kluwer Academic Publishers, New York, USA, 227-241, 2002.
- [13] Yau S. K., Ryan J., Boron toxicity tolerance in crops: A viable alternative to soil amelioration, *Crop Sci.*, 48, 854-865, 2008.
- [14] Reid R., Can we really increase yields by making crop plants tolerant to boron toxicity?, *Plant Sci.*, 178 (1), 9-11, 2010.
- [15] Power P., Woods G. W., The chemistry of boron and its speciation in plants, *Plant Soil.*, 198, 1-13, 1997.
- [16] Hunt C. D., Boron-binding-biomolecules: A key to understanding the beneficial physiologic effects of dietary born from prokaryotes to humans, In: *Boron in Plant and Animal Nutrition* (H.E. Goldbach, B. Rerkasem, M.A. Wemmer, P.H. Brown, M. Thellier, and R.W. Bell, eds) Kluwer Academic, New York, USA, pp. 21-36. 2002.
- [17] Morgan V., Geochemistry, In: *Supplement to Mellor's Comprehensive Treatise on Inorganic and Theoretical Chemistry*, Chemistry, vol. Part A: Boron-Oxygen Compounds, Longman, New York, 1980.
- [18] EPA, Health and environmental effects document for boron and boron compounds, U.S. Environmental Protection Agency, Washington, D.C. EPA 6008-91015, 1991.
- [19] Bassett R. L., The geochemistry of boron in thermal water, Ph.D. thesis, Stanford University, Stanford Calif., 1976.
- [20] Elrashidi M. A., O'Connor G.A., Boron sorption and desorption in soils, *Soil Sci. Soc. Am. J.*, 46, 27-31, 1982.
- [21] Keren R., Mezuman U., Boron adsorption by clay minerals using a phenomenological equation, *Clays Clay Miner.*, 29, 198-203, 1981.
- [22] Couch E. L., Grim R.E., Boron fixation by illites, *Clays Clay Miner.*, 16, 249-256, 1968.
- [23] Sims J. R., Bingham E. T., Retention of boron by layer silicates, sesquioxides, and soil materials: II. Sesquioxides, *Soil Sci. Soc. Am. Proc.*, 32, 364-369, 1968.
- [24] Goldberg S., Glaubing R. A., Boron adsorption on aluminium and iron oxide minerals, *Soil Sci. Soc. Am. J.* 49:1374-1379, 1985.
- [25] Rhoades J. D., Ingvalson R. D., Hatcher J. T., Adsorption of boron by ferromagnesian minerals and magnesium hydroxide, *Soil Sci. Soc. Am. Proc.*, 34, 938-941, 1970.
- [26] Gu B., Lowe L. E., Studies on the adsorption of boron on humic acids, *Can. J. Soil Sci.*, 70, 305-311, 1990.
- [27] Lemarchand E., Schott J., Gaillardet J., Boron isotopic fractionation related to boron sorption on humic and the astructure of surface complexes formed, *Geochimica et Cosmochimica Acta*, 69, 3519-3533, 2005.
- [28] Yermiyahu U., Keren R., Chen Y., Boron sorption on compost organic matter, *Soil Sci. Soc. Am. J.*, 52, 1309-1313, 1988.

- [29] Sartaj M., Fernandes L., Adsorption of boron from landfill leachate by peat and the effect of environmental factors, *J. Environ. Eng. Sci.*, 4, 19-28, 2005.
- [30] Garat A., Meyer B., A study of different manures and their relationship with boron, *Agrochimica*, 27, 531438, 1983.
- [31] Hue N.V., Hirunburana N., Fox R.L., Boron status of Hawaiian soils as measured by B sorption and plant uptake, *Commun. Soil Sci. Plant Anal.*, 19, 517528, 1988.
- [32] Mascarenhas H. A. A., Miranda M. A. C. D., Bataglia O. C., Pereira J.C.V.N.A., Tanaka R.T., Boron deficiency in soybeans, *Bragantia* 47, 325332, 1988.
- [33] Liu Z., Zhu Q., Tang L., Regularities of content and distribution of boron in soils, *Acta Pedologica Sinica*, 26, 353361, 1989.
- [34] Valk G. G. M. van der, Bruin P. N. A., Nutrition of tulips on fresh soil, Boron application limits early losses, *Bloembollencultuur*, 100, 4445, 1989.
- [35] Berger K. C., Pratt P.F., Advances in secondary and micro-nutrient fertilization, In: *Fertilizer technology and used* (M.H. McVickar G.L. Bridger, and L.B. Nelson, eds.), *Soil Sci. Soc. Am. ASA, Madison, WI*, pp. 281-340, 1963.
- [36] Yermiyahu U., Keren R., Chen Y., Boron sorption by soil in the presence of composted organic matter, *Soil Sci. Soc. Am. J.*, 59, 405-409, 1995.
- [37] Yermiyahu U., Keren R., Chen Y., Effect of compost organic matter on boron uptake by plants, *Soil Sci. Soc. Am. J.*, 65, 1436-1441, 2001.
- [38] Blagojevic S., Zarkovic B., Influence of longterm fertilization on the content of available iron and microelements in a calcareous chernozem soil, *Zbornik Radova Poljoprivrednog Fakulteta, Univerzitet u Beogradu*, 35, 2534, 1990.
- [39] Pakrashi A. C., Haldar M., Effect of moisture regime and organic matter application on the changes in hws B an acid soil of terai region of North Bengal, *Environ. Ecology.*, 10, 292296, 1992.
- [40] Goldberg S., Corwin D. L., Shouse P. J., Suarez D.L., Prediction of boron adsorption by field samples of diverse textures, *Soil Sci. Soc. Am. J.*, 69, 1379-1388, 2005.
- [41] Mezman U., Keren R., Boron adsorption by soils using a phenomenological adsorption equation, *Soil Sci. Soc. Am. J.*, 45, 722-726, 1981.
- [42] Communar G., Keren R., Rate-limited boron transport in soils: Effect of soil texture and solution pH, *Soil Sci. Soc. Am. J.*, 70, 882-892, 2006.
- [43] Communar G., Keren R., Equilibrium and nonequilibrium transport of boron in soil, *Soil Sci. Soc. Am. J.*, 69, 311-317, 2005.
- [44] Shani U., Dudley L. M., Hanks R. J., Model of boron movement in soils, *Soil Sci. Soc. Am. J.*, 56, 1365-1370, 1992.
- [45] Goldberg S., Lesch S. M., Suarez D.L., Predicting boron adsorption by soils using chemical parameters in the constant capacity model, *Soil Sci. Soc. Am. J.*, 64, 1356-1363, 2000.
- [46] Vaughan P. J., Shouse P. J., Goldberg S., Suarez D. L., Ayars J.E., Boron transport within an agricultural field: Uniform flow versus mobile-immobile water model simulations, *Soil Sci.*, 169, 401-412, 2004.
- [47] Shouse P.J., Goldberg S., Skaggs T.H., Soppe W.O., Ayars J.E., Effect of shallow groundwater management on the spatial and temporal variability of boron and salinity in an irrigation field, *Vadose Zone J.*, 5, 377-390, 2006.
- [48] Communar G., Keren R., Effect of transient irrigation on boron transport in soils, *Soil Sci. Soc. Am. J.*, 71, 306-313, 2007.
- [49] Ben-Gal A., Shani U., Effect of excess boron on tomatoes under water stress, *Plant Soil*, 256, 179-186, 2003.
- [50] Tripler E., Medjool date palm tissue culture under combined excess of boron and salinity stress, MS thesis, Hebrew University of Jerusalem, Rehovot, Israel, (Hebrew), 2004.
- [51] Tripler E., Ben-Gal A., Shani U., Consequence of salinity and excess boron on growth, evapotranspiration and ion uptake in date palm (*Phoenix Dactylifera* L., cv. Medjool), *Plant Soil.*, 297, 147-155, 2007.
- [52] Dell B., Huang L., Physiological response of plants to low boron, *Plant Soil*, 193, 103-120, 1997.
- [53] Parr A.J., Loughman B.C., Boron and membrane function in plants, (D.A. Robb and W.S. Pierpoint, eds), Academic Press, New York, pp 87-107, 1983.
- [54] Lukaszewski K. M., Blevins D.G., Root growth inhibition in boron-deficient or aluminium-stressed squash may be a result of impaired ascorbate metabolism, *Plant Physiol.*, 112, 1135-1140, 1996.
- [55] Marschner H., *Mineral Nutrition of Higher Plants.*, Academic Press, SAN Diego, USA, pp 379-396, 1995.
- [56] Hu H., Brown P.H., Absorption of boron by plant roots, *Plant Soil.*, 193, 49-58, 1997.
- [57] Biela A., Grote K., Otto B., Hoth S., Hedrich R., Kaldenhoff R., The Nicotiana tabacum plasma membrane aquaporins in NtAQP1 is mercury-insensitive and permeable for glycerol, *Plant J.*, 18, 565-570, 1999.
- [58] Gerbeau P., Güclü J., Ripoche P., Maurel C., Aquaporin Nt-TIPa can account for the high permeability of tobacco cell vacuolar membrane to small neutral solution, *Plant J.* 18, 577-587, 1999.
- [59] Dordas C., Chrispeels M. J., Brown P.H., Permeability and channel-mediated transport of boric acid across membrane vesicles isolated from squash roots, *Plant Physiol.*, 124, 1349-1361, 2000.
- [60] Bastías E. I., Fernández-García N., Carvajal M., Aquaporin functionality in roots of *Zea mays* in relation to the interactive effects of boron and salinity, *Plant Biol.*, 6, 415-421, 2004.
- [61] Reid R. J., Understanding the boron transport network in plants, *Plant Soil.*, 385, 1-13, 2014.
- [62] Brown P. H., Shelp B. J., Boron mobility in plants, *Plant Soil.*, 193, 85-101, 1997.
- [63] Miwa K., Fujiwara T., Boron transport in plants: Co-

- ordinated regulation of transporters, *Annals of Botany*, 105 (7), 1103-1108, 2010.
- [64] Reid R. J., Hayes J. E., Posti A., Stangoulis J. C. R., Graham R.D., A critical analysis of the causes of boron toxicity in plants, *Plant, Cell Environ.*, 27, 1405-1414, 2004.
- [65] Brown P.H., Hu H., Phloem mobility of boron is species dependent: Evidence for phloem mobility in sorbitol-rich species, *Ann. Bot.*, 77, 497-505, 1996.
- [66] Reid R. J., Boron toxicity and tolerance in crop plants, In: Tuteja N, Gill SS (eds) *Crop improvement under adverse conditions*, Springer, New York, pp 333-346, 2013.
- [67] Eaton F. M., Blair G.Y., Accumulation of boron by reciprocally grafted plants, *Plant Physiol.*, 10, 411-424, 1935.
- [68] Nable R.O., Resistance to boron toxicity amongst several barley and wheat cultivars: A preliminary examination of the resistance mechanism, *Plant Soil.*, 112, 45-57, 1988.
- [69] Ben-Gal A., The contribution of foliar exposure to boron toxicity, *J. Plant Nutr.*, In press, 2007.
- [70] Maldonado J. M., Navarro-Gochicoa M. T., Role of boron in vascular plants and response mechanisms to boron stresses, *Plant Stress*, 4 (2), 115-122 2010.
- [71] Loomis W. D., Durst R. W., Chemistry and biology of boron, *Biofactors* 3 (4), 229-239, 1992.
- [72] Wimmer M. A., Mühling K. H., Läuchli A., Brown P. H., Goldbach H. E., Boron toxicity: The importance of soluble boron, pp. 241- 253, In: *Boron in Plant and Animal Nutrition* (H.E. Goldbach, B. Rerkasem, M.A. Wimmer, P.H. Brown and R.W. Bell, eds), Kluwer Academic Publishers, New York, USA, 2002.
- [73] Gupta U. C., Relationship of total and hot-water soluble boron, and fixation of added boron, to properties of Podzol soils, *Soil Sci. Soc. Am. Proc.*, 32, 45-48, 1968.
- [74] Biggar J. W., Fireman M., Boron adsorption and release by soils, *Soil Sci. Soc. Amer. Proc.*, 24, 115-120, 1960.
- [75] Fleming G. A., Essential micronutrients, I: Boron and molybdenum. pp. 155-197, In: *Applied soil trace elements* (B.E. Davis, ed.), John Wiley and Sons, New York, USA, 1980.
- [76] Yau S. K., Interactions of boron-toxicity, drought, and genotypes on barley root growth, yield, and other agronomic characters *Aust. J. Agric. Res.* 53, 347-54, 2002.
- [77] Shani U., Hanks R. J., Model of integrated effects of boron, inert salt, and water flow on crop yield, *Agronomy J.*, 85, 713-717, 1993.
- [78] Hamurcu M., Demiral T., Hakki E. E., Turkmen Ö., Gezgin S., Bell R. W., Oxidative stress responses in watermelon (*Citrullus lanatus*) as influenced by boron toxicity and drought, *Zemdirbyste-Agriculture*, 102 (2), 209-216, 2015.
- [79] Marcar N. E., Guo J., Crawford D.F., Response of *Eucalyptus camaldulensis* Dehnh., *E. globulus* Labill. ssp. *globulus* and *E. grandis* W. Hill to excess boron and sodium chloride, *Plant Soil*, 208, 251-257, 1999.
- [80] Wimmer M. A., Mühling K.H., Läuchli A., Brown P.H., Goldbach H.E., The interaction between salinity and boron toxicity affects the subcellular distribution of ions and proteins in wheat leaves, *Plant, Cell Environ.*, 26, 1267-1274, 2003.
- [81] Piccioni G. A., Karaca H., Boyse L. G., McCaslin B. D., Herrera E. A., Salinity, boron, and irrigated pecan productivity along New Mexico's Rio Grande Basin, *J. Environ. Qual.*, 29, 955-963, 2000.
- [82] Nicholaichuk W., Leyshon A. J., Jame Y. W., Campbell C. A., Boron and salinity survey of irrigation projects and the boron adsorption characteristics of some Saskatchewan soils, *Can. J. of Soil Sci.*, 68, 77-90, 1988.
- [83] Feigin A., Ravina I., Shalhevet J., *Irrigation with Treated Sewage Effluent*, Springer Verlag, New York, 1991.
- [84] Keren R., O'Connor G. A., Effect of exchangeable ions and ionic strength on boron adsorption by montmorillonite and illite, *Clays Clay Miner.*, 30, 341-346, 1982.
- [85] Kemp P. H., *The Chemistry of borates (Part 1)*, Borax Consolidated Ltd., London, 90 pp., 1956.
- [86] Bernstein L., Effects of salinity and sodicity on plant growth, *Ann. Rev. Phytopath.*, 13, 295-312, 1975.
- [87] Munns R., Termaat A., Whole-plant responses to salinity, *Aust. J. Plant Physiol.*, 13,143-160, 1986.
- [88] Bingham F. T., Strong J. E., Rhoades J.D., Keren R., Effect of salinity and varying boron concentration on boron uptake and growth of wheat, *Plant Soil*, 97, 345-351, 1987.
- [89] Mikkelsen R. L., Haghnia G. H., Page A. L., Bingham F.T., The influence of selenium, salinity, and boron on alfalfa tissue composition and yield, *J. Environ. Qual.*, 17, 85-88, 1988.
- [90] Grattan S.R., Shannon M.C., Grieve C.M., Poss J.A., Suarez D., Leland F., Interaction effects of salinity and boron on the performance and water use *Eucalyptus*, *Acta Hort.*, 449, 607-613, 1997.
- [91] Holloway R. E., Alston M., The effects of salt and boron on growth of wheat, *Aust. J. Agric. Res.*, 43, 987-1001, 1992.
- [92] Grieve C. M., Poss J. A., Wheat response to interactive effects of boron and salinity, *J. Plant Nutr.*, 23, 1217-1226, 2000.
- [93] Alpaslan M., Gunes A., Interactive effects of boron and salinity stress on the growth, membrane permeability and mineral composition of tomato and cucumber plants, *Plant Soil*, 236, 123-128, 2001.
- [94] Ben-Gal A., Shani U., Yield, transpiration and growth of tomatoes under combined excess boron and salinity stress, *Plant Soil.*, 247, 211-221, 2002.
- [95] Yadav H. D., Yadav O. P., Dhankar O. P., Oswal M. C., Effect of chloride salinity and boron on germination, growth, and mineral composition of chickpea (*Cicer arietinum* L.), *Annals of Arid Zone.*, 28, 63-67, 1989.
- [96] Yermiyahu U., Ben-Gal A., Sarig P., Zippilevitch E., Boron toxicity in grapevine (*Vitis vinifera* L.) in conjunction with salinity and rootstock effects, *J. of Hortic. Sci. and*

- Biotech., 82, 547-554, 2007.
- [97] Yermiyahu U., Ben-Gal A., Keren R., Reid R. J., Combined effect of salinity and excess boron on plant growth and yield, *Plant Soil.*, 304, 73-87, 2008.
- [98] Masood S., Wimmer M. A., Witzel K., Zörb C., Mühling K.H., Interactive effects of high boron and NaCl stresses on subcellular localization of chloride and boron in wheat leaves, *J. Agro. Crop Sci.*, 198, 227-235, 2012.
- [99] Wimmer M. A., Goldbach H. E., Boron-and-salt interactions in wheat are affected by boron supply, *J. plant nutria and soil sci.*, 175 (2), 171-179, 2012.
- [100] Bastía E., Alcaraz-López C., Bonilla I., Martínez-Ballesta M. C., Bolaños L., Carvajal M., Interactions between salinity and boron toxicity in tomato plants involve apoplastic calcium, *J. Plant Physiol.*, 167 (1), 54-60, 2010.
- [101] del Carmen Rodríguez-Hernández M., Moreno D.A., Carvajal M., Ballesta M. D. C. M., Interactive effects of boron and NaCl stress on water and nutrient transport in two broccoli cultivar,. *Functional Plant Biol.*, 40 (7), 739-748, 2013.
- [102] Grieve C. M., Poss J. A., Grattan S. R., Suarez D. L., Smith T. T., The combined effects of salinity and excess boron on mineral ion relations in broccoli, *Sci. Hort.*, 125, 178-187, 2010.
- [103] Smith T. E., Grattan S. R., Grieve C. M., Poss J. A., Suarez D. L. Salinity's influence on boron toxicity in broccoli, I: Impacts on yield, biomass distribution, and water use, *Agric. Water Mgmt.*, 97, 777-782, 2010
- [104] Smith T. E., Grattan S. R., Grieve C. M., Poss J. A., Suarez D. L., Salinity's influence on boron toxicity in broccoli, II: Impacts on boron uptake, uptake mechanisms and tissue ion relations, *Agric. Water Mgmt.*, 97, 783-791, 2010.
- [105] Smith T. E., Grattan S. R., Grieve C. M., Poss J. A., Läuchli A. E., Suarez D. L., pH dependent salinity-boron interactions impact yield, biomass, evapotranspiration and boron uptake in broccoli (*Brassica oleracea* L.), *Plant soil*, 370 (1-2), 541-554, 2013.
- [106] Dan J., Gerson R., Koyumdjisky H., Yaalon D., *Aridic Soils of Israel; Properties, Genesis and Management*, Special Publication No. 190 Agricultural Research Organization, The Volcani Center, Bet Dagan, Israel, 1981.
- [107] Yermiyahu U., Ben-Gal A., Sarig P., Boron toxicity in grapevines, *Hort Sci.*, 41, 1698-1703, 2006.
- [108] Maas E. V., Crop salt tolerance, pp. 262-304, In: *Agricultural Salinity Assessment and Management*, (Tanji, ed.) ASCE Manuals and Reports on Engineering No 71, ASCE, New York, 1990.