

Salinity's influence on boron toxicity in broccoli: I. Impacts on yield, biomass distribution, and water use

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ARTICLE INFO

Article history:

Received 18 June 2009

Accepted 15 January 2010

Keywords:

Combined stressors

Salinity

Water reuse

ABSTRACT

Research addressing the interactive effects of the dual plant stress factors, excess boron and salinity, on crop productivity has expanded considerably over the past few years. The purpose of this research was to determine and quantify the interactive effects of salinity, salt composition and boron (B) on broccoli (*Brassica oleracea* L.) fresh head yield, biomass distribution and consumptive water use. A greenhouse experiment was conducted using a sand-tank system in which salinity–B treatment solutions were supplemented with a complete nutrient solution. Chloride-dominated salinity and salinity characteristic of California's San Joaquin valley (SJV), or sulfate-dominated, were tested at EC_w levels of 2, 12 and 19 dS m⁻¹. Each salinity treatment consisted of boron treatments of 0.5, 12 and 24 mg L⁻¹. Plant head yield and shoot biomass were significantly reduced by both salinity and boron. Moreover, there was a significant salinity–boron interaction where increased boron was relatively less detrimental under saline conditions. These results occurred regardless of the salt solution composition (chloride or SJV). We found that an 'interactive model' better described our growth response than did a 'single stressor yield model'. Salinity and boron also affected the distribution of shoot biomass. Regardless of salt type, as salinity increased, the fraction of biomass as leaf tissue increased while the biomass fraction as stems and particularly heads, decreased. However, an increase in B at low or high salinity with the SJV composition, decreased the head biomass fraction. This was not observed at moderate salinity, nor on any plants treated with Cl-dominated salinity. Cumulative evapotranspiration (ET) was also reduced by increased salinity but water use efficiency (WUE) was not. WUE was reduced by increased boron, but only at the low and high salinity levels.

Published by Elsevier B.V.

1. Introduction

Many research studies have addressed crop response to the individual stress factors, salinity or boron independently of one another. More recently, the co-occurrence of boron and salinity in natural and agricultural environments has led to many research reports on the interactions of these combined stresses as they affect crop performance (Ben-Gal and Shani, 2002; Nicholaichuk et al., 1988; Yermiyahu et al., 2008).

When both stresses occur together, studies have shown that salinity may reduce or increase boron's toxic effect (Yermiyahu et al., 2008). Some studies have shown that increased salinity can increase boron-related toxic effects, in crops such as tomato, cucumber and wheat (Alpaslan and Gunes, 2001; Grieve and Poss,

2000; Wimmer et al., 2003, 2005). On the other hand, increases in salinity decreased boron toxicity in numerous vegetables, *Prunus* rootstocks, wheat and chickpeas (El-Motaium et al., 1994; Ferreyra et al., 1997; Holloway and Alston, 1992; Yadav et al., 1989).

High soil boron concentration is a concern for several reasons. First, boron is an element that is essential for crops but has a narrow concentration range between that what is considered deficient and that which is potentially toxic (Marschner, 1995). Second, elevated and potentially toxic levels of soil boron are commonly associated with saline soils in many regions of the world, including Chile (Bastías et al., 2004; Ferreyra et al., 1997), Saskatchewan, Canada (Nicholaichuk et al., 1988), Western Fresno County, CA (Bañuelos et al., 2003; Bañuelos, 2002), India (Sharma et al., 1993), Upper Eyre Peninsula, Australia (Holloway and Alston, 1992), and the Rio Grande Basin, New Mexico (Picchioni et al., 2000). Third, boron has a higher affinity to the soil than common salts, usually requiring more water to reclaim soil boron to non-damaging levels than to reduce the salinity to optimum levels (Ayers and Westcott, 1985). Finally, reuse of saline drainage water is a management option that is necessary for reducing the volume

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of drainage water produced on the west side of California's San Joaquin Valley (SJV). A potential limitation in implementing a drainage water reuse system in this region is the extent by which boron, a naturally occurring element in the drainage water, affects the selection, growth and yield of crops in the reuse system. Boron concentration in SJV's saline drainage water varies widely but in most areas, far exceeds levels that would result in toxic conditions based on boron tolerance guidelines (Maas and Grattan, 1999). Therefore understanding how plants respond to high soil boron concentrations in the presence of salinity is necessary to better manage crop performance under field conditions.

Expressions that predict relative crop yields based on soil salinity were developed under conditions of low boron and coefficients that describe this response are listed for nearly 100 crops (Maas and Grattan, 1999). Conversely, relative yield models related to boron concentration in the soil water are rather limited and were done under non-saline conditions (Bingham et al., 1985; Francois, 1986).

Broccoli is an economically important vegetable produced commercially on the Westside of the SJV. The crop is moderately sensitive to salinity according to the yield response parameters determined by the Maas–Hoffman threshold-slope model. Based on biomass accumulation, the threshold electrical conductivity of the soil saturated extract that does not reduce yield below that obtained under non-saline conditions is 2.8 dS m^{-1} ; the slope is 9.2% (Maas and Grattan, 1999). The salt tolerance parameters based on head yield are reported as: threshold = 1.28 dS m^{-1} ; slope = 15.8% (De Pascale et al., 2005). Broccoli is also moderately sensitive to B based on marketable head weight in non-saline conditions: threshold = 1.0 mg B L^{-1} ; slope = 1.8% (Francois, 1986).

Crops under field conditions often endure multiple stresses as they grow and mature and the interactive effects of these factors on crop growth and yield should be the focus of future research (Mittler, 2006; Läuchli and Grattan, 2007). Therefore, the response functions described above may not be appropriate for crops grown in the field under conditions where two or more stresses occur simultaneously. A limited amount of research has examined or modeled the effects of multiple stressors on crop performance including salinity in combination with boron (Shani et al., 2005), flooding (Barrett-Lennard, 2003), water deficit (Homaee et al., 2002), nutrient imbalances (Grattan and Grieve, 1999) and pathogens (Snapp et al., 1991). While studying salinity and boron stress, Ben-Gal and Shani (2002) and Shani et al. (2005), concluded that the dominant stress controls the yield function. They found that when both stresses were present, salinity was the dominant stressor until increasing boron concentrations reached a level that was more damaging, thereby overshadowing salinity's adverse effect. While this expression describes their data well, their model assumes no interaction between salinity and boron, which is often reported in salinity–boron experiments. Salinity and boron interactions, when present, are a conditional relationship where the relative yield or other dependent variable varies according to salinity and boron concentration. The regression lines for relative yield (or other dependent variables) have different slopes and/or intercepts for salinity and boron concentration.

Terminology describing interactive relationships, including positive, negative, additive, synergistic and antagonistic are relative and often confusing (Grattan and Grieve, 1999). Negative or positive relationships are sometimes used to indicate the slope of the regression and other times to describe the effect on yield. Synergistic interactions suggest a greater impact on the dependent variable than the additive effects; antagonistic interactions imply reduced impacts on the independent variable as compared to additive interactions effects.

Salinity effects on yield are well documented, however, the growth and yield reductions from salt type or dominant anion in

the saline media are less understood. Salinity in soils and water is associated with various combinations of sodium, calcium, magnesium, chloride, sulfate and bicarbonate as the dominant ions. Salinity, regardless of its composition, reduces crop growth and yield by osmotic effects but research with salt type and boron toxicity has generated varying results. With wheat as the test crop, Bingham et al. (1987) found no boron interactions with chloride-dominated salinity, as did researchers with corn, barley and alfalfa (Mikkelsen et al., 1988; Shani and Hanks, 1993). Researchers using sulfate-dominated salinity also found no salinity–boron interaction with tall wheatgrass (Diaz and Grattan, 2009). Conversely, other researchers have observed severe leaf injury in wheat associated with excessive boron uptake from chloride-based saline irrigation waters (Grieve and Poss, 2000; Läuchli et al., 2001; Wimmer et al., 2003). Tomato and cucumber have shown greater sensitivity to boron in saline environments (Aspaslan and Gunes 2001). Perhaps the most counter intuitive plant response to salinity stress is increased tolerance to boron toxicity. This response has been documented in numerous crops (Ferreira et al., 2001), eucalyptus (Grattan et al., 1996), pistachio (Ferguson et al., 2002), chickpeas (Yadav et al., 1989) and *Prunus* spp. rootstocks (El-Motaium et al., 1994).

This comprehensive sand-tank study was conducted in a greenhouse to better understand the response and interactions between salinity and boron stresses on broccoli. The purpose of this research was to quantify and evaluate the interactive effects of boron and salinity, including two salt compositions, on broccoli (*Brassica oleracea* L., botrytis group) growth, visual injury, head yield, biomass production, and consumptive water use. A subsequent paper will address the effects on ion relations within the plant including boron uptake and distribution.

2. Materials and methods

A greenhouse experiment, using broccoli (cv. Seminis PX511018), was conducted in sand tanks at the USDA-ARS, U.S. Salinity Laboratory located at the University of California, Riverside campus. The sand-tank system, which consists of 60 large tanks ($1.2 \text{ m} \times 0.6 \text{ m} \times 0.5 \text{ m}$ deep) filled with washed river sand, created a uniform and controlled environment. Tanks were irrigated with solutions prepared in individual reservoirs, each having a volume of approximately 760 L. Salinity–B treatment solutions were supplemented with a complete nutrient solution whose composition is described elsewhere (Carter et al., 2005). Solutions were pumped twice daily from storage reservoirs, located below the sand-tank facility, to the sand tanks and then drainage water returned to the reservoirs by gravity flow. Each reservoir irrigated three replicate tanks. Total evapotranspiration from each tank was measured by solution-volume changes in the storage reservoirs and water lost was replenished daily to maintain constant osmotic potentials in the treatment irrigation waters. Six sand tanks were not planted but were irrigated to provide maximum evaporation rates under this frequently irrigated condition.

The irrigation treatments consisted of three salinity levels representing non-saline (2.0 dS m^{-1}), moderately saline (12 dS m^{-1}) and saline (19 dS m^{-1}) conditions. Based on soil water (EC_{sw})–EC_e¹ relations for most mineral soils at 'field capacity' these respective saline treatments translate into average rootzone salinities (EC_e) of 0.7, 5.0 and 8.2 dS m^{-1} . Each salinity level was comprised of either chloride-dominated salts (Cl) or synthetic saline drainage water with an ion composition typical to that found in shallow, saline water tables in the western San Joaquin Valley (SJV) (Table 1). We also refer to this treatment as sulfate-dominated.

¹ EC_{sw} and EC_e refer to the electrical conductivity of the soil water and saturated soil extract, respectively.

Each of these salinity treatments was tested at three boron concentrations ranging from low, such as that found in solution cultures (i.e. 0.5 mg L^{-1}), to high (12 mg L^{-1}) and very high B concentrations (24 mg L^{-1}) that can be found in concentrated drainage water in western SJV. Irrigation waters were analyzed by inductively coupled plasma optical emission spectroscopy (ICPOES) three times during the experiment to confirm that target ion concentrations were maintained.

Broccoli was planted on 4 February, 2003, at a density of 30 plants per tank and salinization began 16 days later when plants had approximately two leaves. Salinization was delayed in order for the plants to become well established and to correct micronutrient deficiencies that were detected shortly after emergence.

During the first few weeks of the study, the pH of the solution was adjusted to 6.0 every 2 days using sulfuric acid. We found that the pH of the solutions rose to about 8.0 over a 2-day period. Between 28 February and 15 April 2003, the pH of the solutions was adjusted to 6.0 approximately every 2 weeks. Thereafter the pH was not adjusted and therefore remained about 8.0 for most of the experimental time.

Broccoli was first sampled and thinned on 28 March, to 18 plants per tank. Broccoli was sampled again on 24 April, and thinned to a final density of 12 plants per tank. On 24 April, total shoot biomass was determined and plants were partitioned into leaf blades, leaf margins, and petioles. The remainder of the plants was harvested at maturity on 21 May (90 days after salinization). Broccoli shoots were divided into heads, stems, young leaves (most fully expanded leaves and younger), mid-stem leaves and bottom leaves (all remaining leaves). Immature heads, from salt-stressed treatments that were not harvested earlier, were given the opportunity to mature and these heads were harvested on 29 May. Fresh and dry weight measurements were made on all harvested biomass.

Standard meteorological measurements were made in the greenhouse with a Class I agrometeorological station. Ambient daytime air temperatures in the greenhouse during the experiment ranged from 14 to $37 \text{ }^\circ\text{C}$ (mean = $28 \text{ }^\circ\text{C}$); nighttime temperatures ranged from 12 to $30 \text{ }^\circ\text{C}$ (mean = $21 \text{ }^\circ\text{C}$). Relative humidity ranged from 41% to 48% with a mean of 45% during the day and night.

3. Results

3.1. Salinity composition

There was no significant treatment effect on broccoli yield, fresh weight, total biomass or water use as a result of the salt composition (statistical data not shown). Plants, responded indifferently, for the most part, to chloride- or sulfate-dominated solutions within respective salinity and boron treatments. Therefore head yield and biomass data from both salt types, at a given boron concentration, were combined.

3.2. Head weight

The analysis of variance (ANOVA) of broccoli head-yield data separated by salinity and boron indicates significant differences

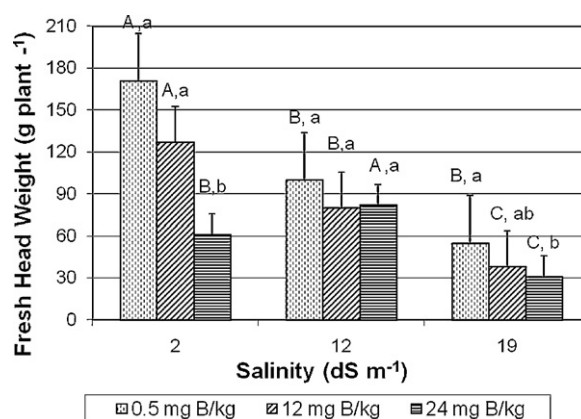


Fig. 1. Broccoli fresh head yields (g plant^{-1}) in response to increasing salinity (2, 12 and 19 dS m^{-1}) and increasing substrate boron levels (0.5 , 12 and 24 mg kg^{-1}). Means with the same upper case letter above a column indicate no significant difference ($P > 0.05$) at a particular boron concentration. Similarly, means with the same lower case letter above a column indicate no significant difference ($P > 0.05$) at a particular salinity level. Data are pooled from both the Cl dominated and SJV salt composition treatments.

($P < 0.05$) among salinity levels, boron concentration, and a significant salinity–boron interaction. Both increased salinity and boron substantially reduced head weights (Fig. 1). At low salinity, increased boron reduced head weights by 64% whereas at high salinity, increased boron only reduced yields by 44%. Therefore when plants were exposed to salinity, relative yield reductions due to increased boron were less even though plants were most adversely affected under the highest combined salinity and boron treatment (Fig. 1). Interestingly at moderate salinity, increased boron did not significantly reduce head yields. Looking at the data from another perspective, at low boron, increased salinity resulted in a 68% reduction in yield. Similar results were found at high boron (12 mg L^{-1}). However at very high boron (24 mg L^{-1}), as salinity increased to moderate levels (12 dS m^{-1}), yield actually increased. This would suggest that salinity, within limits, provides a protective mechanism against B toxicity. However as salinity increased further to 19 dS m^{-1} , yield again declined, presumably because salinity stress is the dominant growth-limiting factor.

Relative broccoli yields were compared in relation to boron in the soil water using the Maas–Hoffman coefficients (Maas and Grattan, 1999). The literature indicates that a solution boron concentration of 12 mg L^{-1} translates into a 20% reduction in yield. We found that head yields were reduced by 26%, which is, in general, comparable considering different environmental conditions in our study versus those reported in the literature. However, as one would expect, the Maas–Hoffman coefficients for boron used to predict relative yield as independent stressor, over-predicts relative yield in the presence of combined salinity and boron stresses. Therefore even though the effects of individual stresses are not additive, both were responsible for reducing head yields.

Table 1

Ionic compositions of waters for the various salinity treatments. SJV refers to San Joaquin Valley or sulfate-dominated water and Cl is chloride-dominated water.

Salt type	ECw (dS m^{-1})	Ca ($\text{mmol}_e \text{L}^{-1}$)	Mg ($\text{mmol}_e \text{L}^{-1}$)	Na ($\text{mmol}_e \text{L}^{-1}$)	K ($\text{mmol}_e \text{L}^{-1}$)	Cl ($\text{mmol}_e \text{L}^{-1}$)	SO ₄ ($\text{mmol}_e \text{L}^{-1}$)
SJV	2	5.3	3.0	4.3	3.0	2.3	6.0
SJV	12	25.6	19.4	76.8	3.0	37.4	79.6
SJV	19	29.6	32.6	134.3	3.0	65.5	127.0
Cl	2	5.2	3.0	6.0	3.0	11.0	2.0
Cl	12	47.7	6.0	48.5	3.0	102.2	2.0
Cl	19	81.2	6.0	85.4	3.0	170.0	2.0

Table 2

Broccoli dry shoot biomass in relation to variable salinity and boron treatments. Means with the same upper case letter within columns indicate no significant ($P > 0.05$) salinity difference at a particular boron concentration. Similarly, means with same lower case letters across rows are not statistically significant ($P > 0.05$) for boron at a particular salinity level. Yield data from both salt composition treatments combined.

ECw (dS m ⁻¹)	Biomass (g plant ⁻¹)		
	Boron (0.5 mg L ⁻¹)	B (12 mg L ⁻¹)	B (24 mg L ⁻¹)
2	106 A,a	91 A,a	56 B,b
12	96 A,a	81 A,ab	75 A,b
19	69 B,a	55 B,b	53 B,b

3.3. Total shoot biomass

The effects of increased boron, increased salinity and their interactions on total shoot biomass were similar to those on head yields except that the negative impact of each stressor and their combination was not as severe. Since the effects on both the fresh and dry shoot weights were the same, only shoot dry weight data are presented here (Table 2). At low B, increased salinity reduced shoot biomass by 34%. Similar reductions were found at 12 mg L⁻¹ B. However at very high boron concentrations (24 mg L⁻¹) in the external solution, increased salinity did not reduce shoot biomass and in fact there was a slight increase in biomass as salinity increased from 2 to 12 dS m⁻¹. Further increases in salinity (i.e. 12–19 dS m⁻¹) reduced shoot biomass to that found in the non-saline treatment. This behavior was similar to that observed with head yields.

3.4. Shoot biomass distribution

The biomass of various organs as a percentage to total shoot biomass was also examined (Fig. 2a and b). The distribution of shoot dry matter was significantly different ($P < 0.05$) among plant organs (i.e. old (bottom) leaves, middle-aged leaves, young (top) leaves, stems and heads). Increased salinity, regardless of salt type, affected the dry matter partitioning in the shoot. Both salt composition types affected shoot biomass partitioning in more or less the same manner. As salinity increased, a greater proportion of

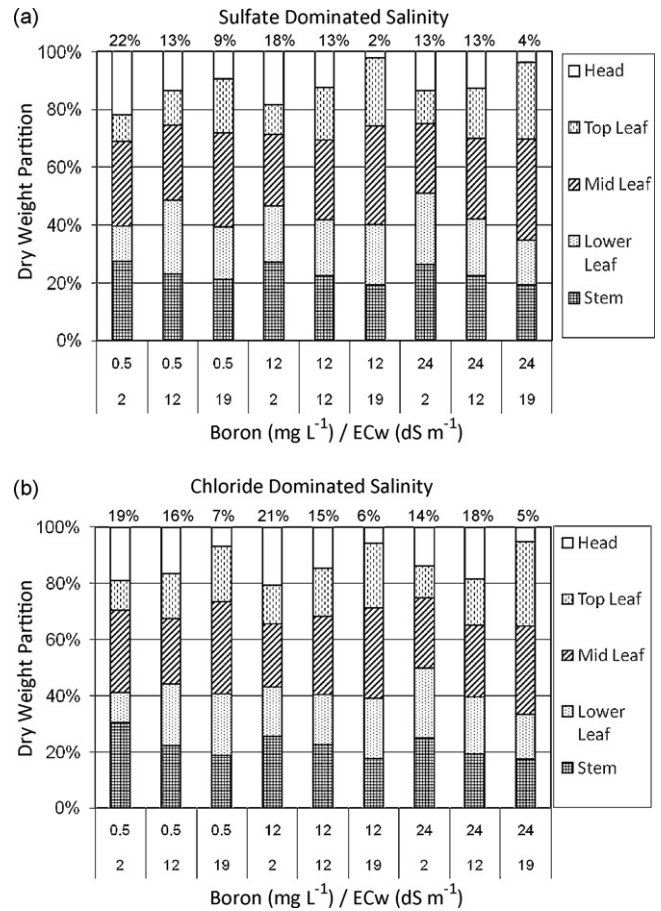


Fig. 2. (a and b) Dry matter partitioning in shoot among heads, top leaves, mid stem leaves, lower leaves and stems. Data in (a) represent effects from the SJV salt-composition treatment while (b) represents those from the Cl-dominated treatment. The values are percentages of the total shoot dry biomass. The numbers at the top of the columns indicate the percentages comprised of heads.

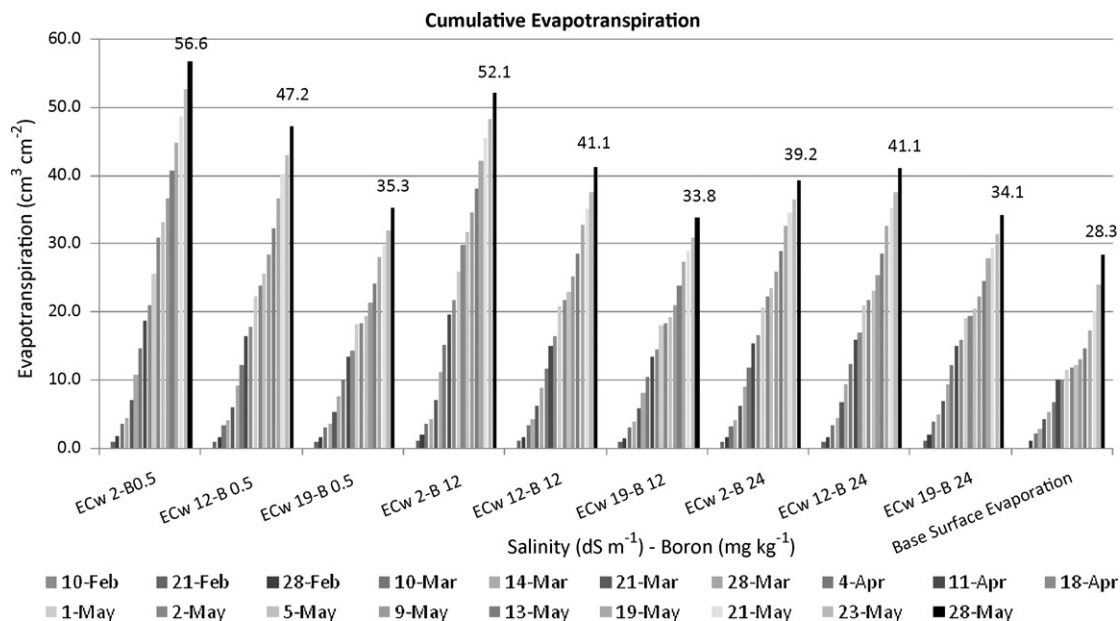


Fig. 3. Cumulative evapotranspiration from salinity and boron treated plots for experimental period of 10 February through 29 May, 2003. Bare surface evaporation refers to the cumulative evaporation from sand tanks not planted to broccoli. Numbers at the top of columns indicates the cumulative ET total for that treatment.

biomass was found in the leaves at the expense of stems and most importantly reproductive tissue (i.e. the heads). Interestingly, a larger portion of biomass was directed towards younger rather than older leaves. When the data of both salt types are pooled, the percentage of head biomass to shoot biomass decreased by 45 and 70% as salinity increased from 2 to 12 and 2 to 19 dS m⁻¹, respectively (data not shown).

Boron, on the other hand, did not significantly affect dry matter partitioning in the shoot with the exception of low and high salinity in the SJV treatment. Here increasing boron from 0.5 to 24 mg L⁻¹ reduced the head weight percentage from 22 to 13%, respectively (Fig. 2a). This effect was not observed in the Cl-dominated treatment. It was also observed that increased boron at low salinity, increased the percentage of biomass comprised of older (lower) leaves. This was found for both salt types.

3.5. Total evapotranspiration and water use efficiency

Cumulative evapotranspiration (ET) was adversely affected by both salinity and boron concentration (Fig. 3) and ANOVA tests indicated that there was a significant salinity–B interaction ($P < 0.05$). Increased salinity reduced water use at each boron concentration. This was most apparent at the low boron concentration (0.5 mg L⁻¹) where ET was reduced by 34%, but was also observed at the high and very high boron concentrations as well. Increasing boron concentration also had a minimizing effect on plant water use at the low and moderate salinities only (2 and 12 dS m⁻¹). High salinity (19 dS m⁻¹) effectively eliminated the influence of boron on plant water use. This was not the same result as seen with biomass or fresh head weight suggesting that growth reductions by salinity and boron are not simply the product of reduced water uptake and carbon fixing. Regression analysis to evaluate the combined effects of salinity and boron on cumulative ET yielded significance and the equation describing water use was, $ET = 26.8 - 0.45 E_{c} - 0.19 B$ ($r^2 = 0.80$). The units are L plant⁻¹, dS m⁻¹ and mg L⁻¹ for the ET, E_c and boron concentration, respectively.

Data on water use efficiency (WUE) were analyzed by ANOVA and found to be significant ($P < 0.05$) for salinity and boron concentrations (Table 3). WUE is defined here as grams of dry shoot biomass accumulated per liter of ET. At low boron, increased salinity did not significantly reduce WUE. Interestingly at very high boron (24 mg L⁻¹), the water use efficiency increased as salinity increased to 12 dS m⁻¹ but then dropped back down as salinity increased further to 19 dS m⁻¹. Increased boron also reduced WUE even though this effect was not statistically significant at moderate levels of salinity. Total accumulated water use for the salinity and boron treatments were also subjected to ANOVA and found significant, as was the salinity–boron interaction.

Table 3

Mean separation for broccoli water use efficiency (WUE)^a in response to salinity (EC_w) and boron (mg L⁻¹). Means with the same upper case letter within columns indicate no significant ($P > 0.05$) salinity difference at a particular boron concentration. Similarly, means with same lower case letters across rows are not statistically significant ($P > 0.05$) for boron at a particular salinity level. SJV and Cl-dominated salt treatments combined.

EC _w (dS m ⁻¹)	Boron (mg L ⁻¹)		
	Boron (0.5 mg L ⁻¹)	Boron (12 mg L ⁻¹)	Boron (24 mg L ⁻¹)
	WUE (g L ⁻¹)		
2	3.9 A,a	3.8 A,ab	3.1 B,b
12	4.2 A,a	4.2 A,a	3.9 A,a
19	4.2 A,a	3.5 A,b	3.5 AB,b

^a WUE is defined here as the amount of shoot dry matter produced per liter of water used by the plant (ET).

4. Discussion

The interactive effects of salinity and boron on yield, biomass distribution and water use are interesting and provide insight on several levels. Some researchers have found that plant response to salinity and boron fits the dominant-stressor hypothesis (Ben-Gal and Shani, 2002; Shani et al., 2005; Shani and Dudley, 2001). Their hypothesis asserts that when multiple stressors are present, the dominant stress factor controls plant response until the other factor reaches a level or concentration where it becomes the dominant stressor, thereafter controlling plant response. This model is analogous to Liebig's law of the minimum regarding mineral nutrition of plants.

Although the 'dominant stress factor' may be used as a first approximation, its application to the data from this salinity–boron study does not adequately describe our results because the model does not account for the interactions between boron and salinity on plant response that we observed here. Salinity and boron interactions are widely reported in experiments. These effects can be additive and increase the negative impacts on yield (Alpaslan and Gunes, 2001; Grieve and Poss, 2000; Wimmer et al., 2003) or antagonistic (e.g. El-Motaïum et al., 1994; Ferreyra et al., 1997; Holloway and Alston, 1992; Yadav et al., 1989), leading to an attenuation of the detrimental effect over a range of concentrations.

We found that salinity–boron interactions for broccoli were antagonistic and that the data fit an 'interactive model' more closely than the 'dominant-stressor model'. Multiple regression of EC_w (dS m⁻¹) and boron concentration (mg L⁻¹) in relation to relative head yield (g plant⁻¹) resulted in the equation: $RY \% = 100 - 2.5 E_{c} - 0.29 B^{1.67} + 0.25 E_{c} B$ ($r^2 = 0.75$). From another perspective, the negative impact of salinity on broccoli fresh weight head yield is somewhat linear at low and moderate boron concentrations (0.5–12 mg L⁻¹ B), but does not maintain the linear relationship at very high boron concentrations (24 mg L⁻¹ B). Similarly, Tripler et al. (2007) found that increased boron from 0.3 to 1.5 mmol L⁻¹ substantially reduced yields of date palm but further increases to 3.0 mmol L⁻¹ caused only minor reductions.

It is not clear why the 'interactive model' better fits our data set. However it is likely the plant response to one of the stresses may positively affect the response to the other stress. For example a reduction of shoot biomass by salinity stress will reduce transpiration which may directly or indirectly affect boron uptake, particularly boron uptake is a simple passive process. This effect will be addressed in the sequential paper.

Total biomass was severely impacted by increased boron at low salinity. The biomass decreased approximately 47% as a function of increasing boron concentration from 0.5 to 24 mg L⁻¹ at 2 dS m⁻¹. The negative effects of high boron were greater at low salinity (2 dS m⁻¹) than at higher levels of salinity. At moderate and high salinity, increased boron produced only an approximate 22% decrease in biomass for both boron concentrations. At low boron, we found that 19 dS m⁻¹ salinity (equivalent to 9 dS m⁻¹ soil E_c) reduced shoot biomass by 35%, which is less than the 57% reduction predicted by the Maas–Hoffman coefficients based on shoot growth rather than head yield. However, these coefficients for salinity, used to predict relative shoot yield as an independent stressor, over-predict relative shoot yield in the presence of combined salinity and boron stresses. Moreover, the impact on head yields were considerably more than on shoot biomass suggesting that broccoli is more sensitive to salinity when expressed as fresh head yield than when expressed as shoot biomass, a response that has recently been quantified by De Pascale et al. (2005). This may also indicate that salinity affects the developmental processes in the plant (Läuchli and Grattan, 2007).

It is important to note that at very high boron concentrations (24 mg L^{-1}), an increase in salinity from 2 to 12 dS m^{-1} , significantly increased broccoli yields and shoot total biomass. This would suggest that at this moderate level of salinity (equivalent to about 6 dS m^{-1} if expressed at ECE), somehow plays a protective role against boron toxicity. This effect was not an anomaly since a recent study by our group tested the influence of pH on the salinity–B interaction and substantiated this finding. Our data indicate that this finding occurs under slightly basic pH conditions using sulfate-dominated salinity and not under slightly acidic conditions where Cl is the dominant anion, which has been the characteristics of most other solutions in other salinity–B studies reported in the literature. At this pH, non-dissociated boric acid ($\text{B}(\text{OH})_3$) is the dominant boron species but the solution contains a significant amount of borate ($\text{B}(\text{OH})_4^-$) as well. Clearly more research is needed in this area.

This research study presents several key findings. Broccoli plants can tolerate high levels of boron, particularly in the presence of salinity. There was a significant salinity–boron interaction whereby increased boron was relatively more detrimental at low salinity than it was at higher salinities. Ion composition of the irrigation waters played little role in the overall salinity–boron interaction. Salinity reduced the biomass of all shoot organs but as salinity increased, the fraction of biomass as leaf tissue increased while the biomass fraction as stems and particularly heads, decreased. This was true under both salt compositions. Interestingly, an increase in B at either low or high salinity, decreased the head biomass fraction only in plants treated with simulated SJV drainage water. This was not observed at moderate salinity, nor on any plants treated with Cl-dominated salinity. More research is needed to better understand this unique effect that occurred only under low and high salinity of these sulfate-dominated waters.

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