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Impacts of boron application on maize plants growing under flooded and unflooded conditions

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Abstract

Plants of maize (*Zea mays* L.) were waterlogged for 7 d and irrigated (root application) or sprayed (foliar application) with 0, 1, 3 and 6 mg dm^{-3} of boron. The stability of leaf membranes was assessed by determining leakage of electrolytes from leaf discs exposed to heat (51 °C) and dehydration (40 % PEG). Leaf membranes were more stable to heat than to dehydration. The membranes of waterlogged plants were more injured than those of control plants. Waterlogging reduced contents of dry mass, chlorophyll, soluble proteins, total free amino acids and soluble sugars and leaf relative water content (RWC). Application of boron increased the stability of leaf membranes, chlorophyll, soluble sugars, soluble proteins, amino acids contents, leaf RWC and dry mass accumulation. Foliar boron application was more effective. Application of boron alleviated the deleterious effect of waterlogging.

Additional key words: chlorophyll, leaf relative water content, membrane stability, waterlogging, *Zea mays*.

Introduction

Waterlogging depressed plant growth, the rate of photosynthesis, stomatal conductance, leaf water potential, and chlorophyll and soluble protein contents, but enhanced free amino acids accumulation and increased the stability of leaf membranes (Jackson 1979, Bishnoi and Krishnamoorthy 1992, Gadallah 1995). Waterlogging also decreases the cytokinin content (Burrows and Carr 1969, Bradford 1983a) which also influences plant growth and many physiological processes.

Boron was known to be an essential micronutrient for plant growth and development. The content of boron below or above the optimum range caused

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Abbreviations: Chl - chlorophyll; d.m. - dry mass; FA - foliar application; PEG - polyethylene glycol; RA - root application; RWC - relative water content; SP - soluble proteins; SS - soluble sugars; TAA - total free amino acids; WL - waterlogging.

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significant changes in the activity of numerous enzymes and consequently affects the metabolism of higher plants (Dugger 1983, Al-Yousif *et al.* 1994, Zhenguo *et al.* 1993). Boron influences the auxin content (Pilbeam and Kirkby 1983, Falkler *et al.* 1985) and translocations (Tang and Dela-Fuenta 1986) in plants. Ultrastructural changes (Hirsch and Torrey 1980) and impaired membrane function (Parr and Loughman 1983) affecting ion transport were observed in plants suffering from B deficiency (Goldbach 1985, Blaser-Grill *et al.* 1989, Goldbach *et al.* 1991, Roldan *et al.* 1992).

The aim of the present work was to study the combined effect of waterlogging and boron on the stability of leaf membranes, chlorophyll content, dry matter accumulation, leaf relative water content and soluble carbon and nitrogen compounds in *Zea mays* plants.

Materials and methods

Maize plants (*Zea mays* L.) were grown from seeds in plastic pots containing 1400 g air dry soil [sand/clay 2:1 (v/v)] under field conditions at the experimental farm of the faculty of Science, Assiut University. The plants (five per pot) were twice watered with 100 cm^3 of full Hoagland nutrient solution. Plants grown for 15 d in soil, the water content of which was maintained at the field capacity, were subjected to 7 d of waterlogging as described by Wample and Thornton (1984) and Gadallah (1995). Plants were flooded by maintaining the water or boron solution levels 1 to 2 cm above the soil surface by periodically adding water or boron solution. Control plants (drained) were watered periodically to field capacity. Plants were either irrigated (root application) or sprayed (foliar application) with 0, 1, 3 and 6 mg dm^{-3} of boron solutions. Three pots were assigned at random to each treatment combination.

Membrane stability test was measured according to Blum and Ebercon (1981). Leaf discs of diameter 10 mm were punched out of the upper fully-expanded leaves and washed with deionized water to remove the surface electrolytes. 5 discs of each treatment were placed *1*) in wetted test tubes and heated to 51 °C for 20 min in a water bath then incubated for 20 h at 10 °C (heat test), and *2*) in test tubes with 10 cm^3 of deionized water (controls) or *3*) 40 % PEG 6000 (drought test) and incubated for 20 h at 10 °C, washed three times with deionized water and reincubated with 10 cm^3 deionized water for further 20 h at 10 °C. The electrical conductance was measured at 25 °C after equilibration of samples in a water bath using conductometer *YSI Model 35* (*Spring Instruments Co.*, USA). Following autoclaving at 100 °C for 15 min and re-equilibration at 25°C the conductance was measured a secondly. The degree of injury was calculated according to formula:

$$\text{injury [\%]} = [1 - \frac{1-(T_1/T_2)}{1-(C_1/C_2)}] \times 100$$

where T_1 and T_2 represent the first and second measurements on the treatment samples and C_1 and C_2 the first and second measurements on the control.

For measuring leaf relative water content (RWC), the methods of Weatherley (1950) was used:

RWC [%] = [(fresh mass - dry mass)/(saturated mass - dry mass)] × 100

Chlorophyll *a* and *b* contents were measured spectrophotometrically according to Todd and Basler (1965). For dry matter determination the fresh roots and shoots were dried in an aerated oven at 70 °C to constant mass. Soluble sugars, total free amino acids and soluble proteins were determined according to Dubois *et al.* (1956), Lee and Takahashi (1966), and Lowry *et al.* (1951), respectively.

The relative roles of single factors and their interaction on the parameters tested were evaluated by analysis of variance (F values) and coefficient of determination (η^2 = sum of squares due to the factor/total sum of squares due to treatment combinations; Ostle 1963).

Results

Leaf membranes stability: A 40 % PEG solution applied to leaf discs caused about 29.2 % injury in the leaf membranes from unflooded control plants and 36.7 % injury in those from flooded plants (Table 1). Boron at concentration 3 and especially 6 mg dm^{-3} applied to the roots increased membrane stability to PEG, under both drained and waterlogged conditions. Spraying of control plants with boron (1 to 3 mg dm^{-3}) have the same beneficial effects. On the contrary, spraying with the higher boron concentration (6 mg dm^{-3}) increased injury of both flooded and unflooded plants.

Table 1. Membrane injury [%] caused by dehydration or heat in leaf discs excised from control and waterlogged (WL) *Zea mays* plants. Effect of foliar (FA) or root (RA) application of boron in different concentrations.

Boron	Dehydration				Heat			
[mg dm^{-3}]	RA		FA		RA		FA	
	control	WL	control	WL	control	WL	control	WL
0	29.2	36.7	29.2	36.7	64.9	80.6	64.9	80.6
1	44.5	41.5	24.6	28.6	60.3	72.9	52.0	74.5
3	7.1	37.7	21.6	46.9	54.2	75.6	57.0	67.2
6	12.4	8.9	57.3	54.6	81.8	75.8	70.9	63.5

Heat stress (51 °C) caused about 64 % injury in the membrane of leaves excised from control plants. The injury increased to 80 % under waterlogging condition. Irrigation or spraying with boron increased membrane stability to heat except at the highest boron concentration with the unlogged plants.

Statistical analysis indicated that the single factors and their interaction significantly affected the stability of leaf membranes to dehydration and heat stress. B was predominant in affecting membrane stability to dehydration and the interaction

WL × B was subdominant. The relative share of both factors (WL and B) in affecting membrane stability of boron irrigated plants to heat is nearly equally dominant (η^2 = 0.35 for both). However, membrane stability to heat of plants sprayed with boron was dominantly affected by the interaction (WL × B) followed by WL (η^2 = 0.42 and 0.35, respectively).

Chlorophyll content: Exposure of *Z. mays* plants to waterlogging (Table 2) decreased chlorophyll (Chl) *a* and *b* contents. Boron applications (by either irrigation or spraying) also significantly increased Chl *a* and *b* contents compared to the control. Spraying was more effective than irrigation. The effects of WL and WL × B were non significant for Chl *a* content only in irrigated plants. Chl *a* and *b* contents were predominantly affected by the presence of boron.

Table 2. Effect of waterlogging (WL) and foliar (FA) or root (RA) boron application on Chl *a* and Chl *b* contents [mg g^{-1} (d.m.)] of *Zea mays* leaves.

Boron	Chl *a*				Chl *b*			
[mg dm^{-3}]	RA		FA		RA		FA	
	control	WL	control	WL	control	WL	control	WL
0	0.55	0.48	0.55	0.48	0.58	0.42	0.58	0.42
1	0.79	0.64	0.86	1.35	0.82	0.62	0.75	1.11
3	0.66	0.89	1.11	1.08	0.51	1.40	0.77	2.30
6	1.15	1.20	1.12	1.26	1.23	1.00	0.89	1.30

Growth: Waterlogging depressed shoot and root dry matter accumulation. Although, B treatment also reduced *Zea mays* growth under drained conditions, its application alleviate the deleterious effect of waterlogging on plant growth (Table 3). B and WL × B interaction had significant effect on roots dry matter accumulation. However, shoots dry matter was negligably affected by the two factor and their interaction.

Table 3. Effect of waterlogging (WL) and boron foliar (FA) or root (RA) application on dry matter [g $plant^{-1}$] of *Zea mays* shoots and roots.

Boron	Shoot				Root			
[mg dm^{-3}]	RA		FA		RA		FA	
	control	WL	control	WL	control	WL	control	WL
0	1.67	1.23	1.67	1.23	0.90	0.43	0.90	0.43
1	1.17	1.43	0.93	1.40	0.53	0.67	0.40	0.73
3	1.47	1.53	1.23	1.20	0.73	0.73	0.63	0.80
6	1.67	1.40	1.00	1.17	0.80	0.80	0.47	0.40

Leaf relative water content: In the absence of boron, the pattern of diurnal fluctuation in RWC (Table 4) of flooded and drained plants was similar. RWC decreased progressively in the morning towards a minimum followed by slight increase at the late afternoon. Flooded or drained plants receiving different boron concentrations had similar trend of changes in the diurnal pattern of their RWC with few exceptions: *1*) higher RWC was observed at 10.00 in drained B-irrigated plants in contrast to their values at sunrise (7.00) or sunset (19.00); *2*) in drained plants boron application increased RWC at midday (13.00), and *3*) flooded plants sprayed with boron maintained higher RWC from 13.00 to 19.00 (compared to their controls). Statistical analysis indicated that B and WL were the predominant factors that affected RWC and the role of interaction WL × B was subdominant.

Table 4. Effect of waterlogging (WL) and boron foliar (FA) or root (RA) application on the diurnal changes of leaf relative water content of *Zea mays* plants.

Boron		control					WL				
[mg dm^{-3}]		07.00	10.00	13.00	16.00	19.00	07.00	10.00	13.00	16.00	19.00
0	RA	89.1	82.5	67.5	70.9	75.9	88.1	79.1	65.8	63.9	68.9
1	RA	86.9	87.6	69.6	65.4	70.1	86.6	77.2	69.0	67.3	72.1
3	RA	76.3	79.3	77.5	65.4	70.1	78.5	77.2	66.6	66.2	71.2
6	RA	74.0	82.0	73.5	70.6	75.9	75.1	73.1	65.8	65.4	70.2
0	FA	89.1	82.5	67.5	70.9	75.9	88.1	79.1	65.8	63.9	68.9
1	FA	81.4	79.1	68.8	65.1	70.1	84.2	65.7	65.3	64.4	69.4
3	FA	87.8	75.1	66.6	60.5	62.2	84.1	77.8	68.2	74.4	76.1
6	FA	88.0	81.2	72.4	76.3	81.2	86.4	78.0	73.5	81.7	86.7

Soluble proteins, total free amino acids and soluble sugars: In the absence of boron, waterlogging reduced soluble proteins (SP), total free amino acids (TAA), and soluble sugars (SS) contents in shoots and roots of *Zea mays* plants (Table 5). Spraying with boron was more effective in shoots and irrigation in roots in increasing SP and TAA contents in both drained and flooded plants. The enhancement of SS accumulation in shoots and roots was greater under foliar than under root application. The interaction (WL × B) had significant effect on SP (except shoot sprayed with B) and SS in roots and shoots of maize plants. Generally, SP, TAA (in shoots and roots) and SS (in shoots) were predominantly affected by B.

Discussion

Waterlogging increases the sensitivity of membranes to heat and dehydration stresses (Table 1). The differences in the permeability of cell membranes may result from changes in the degree of saturation of fatty acids in the phospho-lipids of cell membranes (Yamada *et al.* 1980). Boron treatments had an important role in maintaining membrane stability. Such effects may be due to the effect of B on the

Table 5. Effect of waterlogging (WL) and foliar (FA) or root (RA) boron application on soluble protein (SP), total free amino acids (TAA), and soluble sugar (SS) contents [mg g^{-1}(d.m.)] of *Zea mays* plants.

	Boron	Shoot				Root			
	[mg dm^{-3}]	RA		FA		RA		FA	
		control	WL	control	WL	control	WL	control	WL
SP	0	73.0	66.2	73.0	66.2	60.4	35.0	60.4	35.0
	1	46.9	35.5	82.4	68.7	36.5	40.9	24.8	18.1
	3	45.6	74.7	80.6	71.1	28.4	32.5	22.3	28.8
	6	120.5	91.9	97.5	79.2	53.9	39.2	28.6	22.6
TAA	0	20.3	19.9	20.3	19.9	16.1	9.0	16.1	9.0
	1	22.2	17.4	29.1	29.0	17.7	13.3	11.9	10.8
	3	14.5	17.2	27.3	13.7	10.9	13.6	6.7	7.3
	6	27.3	21.1	23.9	27.6	11.3	10.0	9.5	7.5
SS	0	68.7	34.7	68.7	34.7	66.4	44.7	66.4	44.7
	1	43.8	37.4	96.9	103.3	52.8	53.3	89.9	40.5
	3	54.7	76.4	88.7	107.6	57.7	54.7	39.8	54.4
	6	47.7	52.6	57.6	81.4	51.1	62.2	70.5	34.3

structural integrity and permeability of cell membranes (Tang and Dela Fuente 1986, Parr and Loughman 1983) or transport and distribution of Ca (Ganmore-Neuman and Davidov 1993, Al-Yousif 1994).

Chlorophyll *a* and *b* content slightly decreased in response to waterlogging (Table 2). Similar results have been recently reported for *Ricinus* plants by Gadallah (1995). The higher Chl content in B-treated plants is in agreements with the findings of Bonilla *et al.* (1990), Bolanos *et al.* (1993) and Liang and Shen (1994). In addition B was found essential for the maintenance of normal structure of chloroplasts under WL (Hudák and Herich 1976).

Content of soluble sugars was lower in flooded plants compared to controls. Such a reduction is probably a result of reduced rate of photosynthesis due to stomatal closure (*e.g.* Bradford 1983b, Bishnoi and Krishnamoorthy 1992), and decreasing Chl content (Table 2). B treated plants had higher amounts of SS is in agreements with the findings of Bonilla *et al.* (1980) and Dugger (1983). Boron enhanced SS especially in flooded plants.

WL reduced SP and TAA contents (Table 5). This reduction could be due to decreased synthesis and increased utilization. SP and TAA contents were higher in B-treated plants, presumably through *1*) increasing incorporation of NO_3^- into amino acids (Wyn Jones *et al.* 1979) through increasing nitrate reductase (Zhenguo *et al.* 1993) and nitrogenase (Gonzalez *et al.* 1988) activities and nitrate uptake (Sanchez Maeso *et al.* 1985), *2*) increasing incorporation of H^3-leucine into protein (Cohen 1979), or *3*) affecting phosphorous metabolism and an energy turnover (Dugger 1983).

Generally, waterlogged plants had lower RWC. This reduction was probably a result of stomatal closure and anatomical destruction of waterlogged roots (Bradford

1983b, Bishnoi and Krishnamoorthy 1992). The importance of boron treatments in diminishing RWC decrease under WL (Table 4) confirming the results of Dave and Kannan (1980) who indicated that boron affected the intercellular water movements. Such effects of boron correlated with enhancing stomatal opening by boron through increasing membrane rigidity of the guard cells (Pollard *et al.* 1977, Bejerano and Itai 1981).

It was noticed that foliar application of boron was mostly more effective than root application. This could be due to more uniform distribution of boron across the leaf surface (Schon and Blevins 1990, Shu *et al.* 1994) and/or enhancing stomatal penetration (Biddulph 1960, Hull 1970). B applied to roots is primarily transported by the transpiration stream, which might cause toxic accumulation of B along leaf veins and at the leaf margins (Oertli and Roth 1969, Michael *et al.* 1969).

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