Journal of Plant Nutrition
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713597277

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Online publication date: 06 June 2002

To cite this Article Sotiropoulos, Thomas E. , Therios, Ioannis N. , Dimassi, Kortessa N. , Bosabalidis, Artemios and Kofidis, Georgios(2002) 'NUTRITIONAL STATUS, GROWTH, CO_2 ASSIMILATION, AND LEAF ANATOMICAL RESPONSES IN TWO KIWIFRUIT SPECIES UNDER BORON TOXICITY', Journal of Plant Nutrition, 25: 6, 1249 — 1261
To link to this Article: DOI: 10.1081/PLN-120004386
URL: http://dx.doi.org/10.1081/PLN-120004386

JOURNAL OF PLANT NUTRITION, 25(6), 1249–1261 (2002)

NUTRITIONAL STATUS, GROWTH, CO_2 ASSIMILATION, AND LEAF ANATOMICAL RESPONSES IN TWO KIWIFRUIT SPECIES UNDER BORON TOXICITY

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ABSTRACT

Two *Actinidia* species [*Actinidia deliciosa* (A.Chev.) C.F. Liang et A.R. Ferguson var. *deliciosa* cv. Hayward] and (*Actinidia arguta* Planch.) were grown in a sand-perlite mixture (1 : 1) in a growth room and irrigated with Hoagland's nutrient solutions containing 20, 50, 100, 200, and 500 μM boron (B). Growth, leaf ion concentration, photosynthetic rate and B induced changes in leaf anatomy were investigated. The greatest shoot length of the two species was recorded with 50 μM B. Boron concentration was highest in the leaf margin, intermediate in the remaining leaf blade and minimum in petioles. Boron toxicity

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induced a decrease of photosynthetic rate (Pn), of the volume of mesophyll cells, an increase of the volume of intercellular spaces and cell damage. Inclusion of 500 μM of B in the nutrient solution decreased calcium (Ca) and manganese (Mn) concentrations in kiwifruit leaves but did not affect the concentration of other mineral nutrients. Finally, the two species did not differ significantly in leaf B accumulation and sensitivity to B.

INTRODUCTION

Boron toxicity is a nutritional disorder that can decrease plant growth and productivity in arid and semiarid environments throughout the world. Boron toxicity generally occurs under the following conditions: 1) in soils inherently high in B, 2) in soils over-fertilized with minerals high in B, 3) in soils receiving fossil combustion residues, 4) in soils being used as disposal sites of B-containing waste materials and 5) in soils being irrigated with water high in B content (1).

Kiwifruit is very sensitive to excess B, demanding irrigation water with less than 0.5 mg B L^{-1} (2). Its sensitivity to B is associated with its high transpiration rate (3) and also to its inability to control B absorption and/or transport (4).

During the last decades, B nutrition has been implicated in several areas of plant metabolism like cell wall biosynthesis (5), plasmalemma permeability (6), cell division (7) and auxin action (8). The effect of B nutrition on photosynthesis has rarely been studied. Boron toxicity may indirectly affect photosynthesis by decreasing the photosynthetic leaf area and by altering leaf constituents (9). In the case of B toxicity in peach (*Prunus persica* L. Batsch) leaves, shrinkage and deorganisation of the cells of the spongy parenchyma were observed (10).

The objectives of the present study were to investigate the effect of various B concentrations, including toxic ones, on growth, nutritional status, photosynthetic capacity and leaf anatomy of two *Actinidia* species.

MATERIALS AND METHODS

Plant Growth

One-year-old kiwifruit plants of two species [*Actinidia deliciosa* (A.Chev.) C.F. Liang et A.R. Ferguson var. *deliciosa* cv. Hayward] and (*Actinidia arguta* Planch.) uniform in macroscopic characteristics were planted in plastic containers containing 3 l of sand-perlite medium (1 : 1). The experimental plants were maintained in a growth room at $22 \pm 1^{\circ}C$ and light intensity of 550 μmol m^{-2} s^{-1} (16 h light and 8 h dark period). The plants were irrigated daily with 0.2 l of

modified Hoagland's nutrient solutions. Macronutrients were supplied at half strength and micronutrients, except B, at full strength (11). Treatments included five B concentrations (20, 50, 100, 200, and 500 μM), with six single plant replicates per treatment. After seven weeks of growth, when B toxicity symptoms were clearly visible in the plants irrigated with solutions containing 100–500 μM B, the plants were harvested and the growth in length of the main shoot and the total number of leaves per plant were measured.

Photosynthesis

Photosynthetic rate (Pn) and stomatal conductance (g_s) were measured at the end of the experiment using *Actinidia deliciosa* plants. The measurements were made on the first mature leaf (fourth leaf from the apex) from 11 to 12 o'clock with the LI COR-6200 apparatus (LI COR, Inc., Lincoln, NE). The light intensity of the growth room was maintained at 550 μmol m^{-2} s^{-1} (16 h light and 8 h dark period) with fluorescent lamps.

Microscopy

Small pieces of *Actinidia deliciosa* leaf blades from control and 500 μM B treatments were initially fixed for 4 h with 5% glutaraldehyde in 0.025 M phosphate buffer. After rinsing in buffer, the specimens were post fixed for 5 h with 1% OsO_4. For tissue dehydration an acetone series (50–100%) was used, which subsequently was followed by resin infiltration and embeddment (12). Sections (1 μm thick) of plastic embedded leaf segments were obtained on a Reichert OmU_2 ultramicrotome, stained with 1% toluidine blue in 1% borax and photographed in a Zeiss III photomicroscope.

Leaf Ion Concentration

Twenty leaves per sample of both species were separated into petioles, leaf margins (5 mm wide) and the remaining leaf blades. The samples, were initially washed with tap water and then with distilled water, dried in a forced draft oven at 68°C for 72 h and ground in a mill to pass a 30-mesh screen. B was determined by the azomethine-H method (13), phosphorus (P) by the ammonium phosphovanadomolybdate method and potassium (K), Ca, magnesium (Mg), iron (Fe), Mn and zinc (Zn) by atomic absorption spectrometry.

The experimental design used was the completely randomized design with six replications and two factors (B concentration of the solution and *Actinidia*

species). Differences between means of growth parameters, parameters of photosynthetic ability and ion concentration of leaves were evaluated using Duncan's Multiple Range Test at $P \leq 0.05$.

RESULTS

Plant Growth

Boron concentration in solution affected the shoot length, the fresh weight of shoots and the number of leaves per plant of both *Actinidia* species. Plants of both species produced the longest shoots with 50 μM B (Table 1). As the B concentration in solution increased from 50 to 500 μM, the shoot length of the two species decreased. Shoot length of *Actinidia arguta* was significantly less in comparison to length of *Actinidia deliciosa* when boron concentration in solution was 20, 50, and 500 μM. For the rest of the B concentrations, no statistical difference was recorded between the two species. The plants of both species produced the greatest shoot fresh weight with 50 μM B in solution (Table 1). Concerning the number of leaves per plant, B concentration of 20 μM B produced more leaves in comparison to the rest of the B concentrations. As the B concentration in solution increased, the number of produced leaves per plant decreased (Table 1). Boron toxicity symptoms appeared in the leaves of plants irrigated with solutions containing 100, 200, and 500 μM B. The first sign of B

Table 1. The Effect of B Concentration of the Nutrient Solution on the Average Shoot Length, Fresh Weight per Shoot, and Number of Leaves per Plant

Species	B μM	Shoot Length cm	Fresh Weight of Shoot g	Number of Leaves
A. deliciosa	20	105 b[+]	9.30 c	16 a
A. deliciosa	50	126 a	11.90 a	14 b
A. deliciosa	100	99 bc	8.20 de	13 bc
A. deliciosa	200	93 cd	8.80 cd	12 bcd
A. deliciosa	500	85 d	7.60 e	11 cde
A. arguta	20	94 cd	8.10 de	14 b
A. arguta	50	101 bc	10.30 b	13 bc
A. arguta	100	91 cd	7.80 de	11 cde
A. arguta	200	84 d	8.10 de	10 de
A. arguta	500	72 e	6.60 f	9 e

[+]Means within columns with the same letter are not significantly different at $P \leq 0.05$.

toxicity was a yellow-green interveinal and marginal chlorosis which developed on the oldest leaves and progressed to the youngest leaves.

Parameters of Photosynthetic Ability

Boron concentration of the nutrient solution affected photosynthetic rate and internal CO_2 concentration values (Table 2). By raising B concentration from 20 to 50 μM (Pn) increased and attained maximum value. Afterwards, (Pn) decreased. Concerning stomatal conductance, no statistically significant differences were found between the treatments (Table 2). The lowest value of internal CO_2 concentration was measured with 20 μM B in solution. Further increase of B in nutrient solution to 50 μM resulted in an increase of internal CO_2 concentration which attained maximum value and remained almost constant in the rest of the B treatments (Table 2).

Leaf Anatomy

Leaf anatomy measurements were performed in *Actinidia deliciosa* plants irrigated with solutions containing 20 and 500 μM B. Observations on the anatomy of control leaves indicated that leaf lamina has the typical anatomy and consists of the upper epidermis, the lower epidermis and the mesophyll cells, which divided in palisade and spongy parenchyma (Fig. 1). The cells of upper epidermis were greater than those of lower epidermis. The chloroplast distribution in the mesophyll cells was peripheral. The early symptoms of B toxicity are shown in Figure 2. Mesophyll cells began to shrink and their organelles started to deorganize. Subsequently, the volume of the intercellular spaces was increased.

Table 2. The Effect of B Concentration of the Nutrient Solution on Photosynthetic Parameters of *Actinidia Deliciosa*

B μM	Photosynthetic Rate μmol CO_2 m^{-2} s^{-1}	Stomatal Conductance mol m^{-2} s^{-1}	Internal CO_2 Concentration ppm
20	1.84 c[+]	0.074 a	350 b
50	2.53 a	0.074 a	401 a
100	2.07 bc	0.059 a	400 a
200	1.50 d	0.059 a	397 a
500	1.26 d	0.080 a	398 a

[+] Means within columns with the same letter are not significantly different at $P \leq 0.05$.

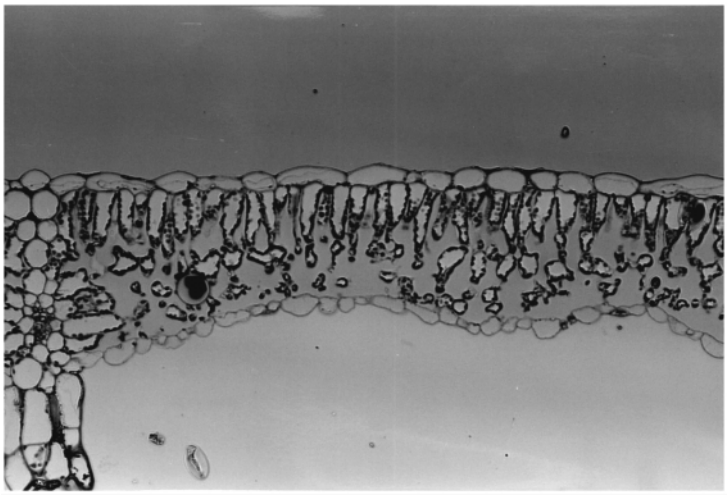

Figure 1. Cross sections (X200) of *Actinidia deliciosa* leaves (control).

However, epidermal cells were not affected by B toxicity. Comparative observations on the anatomy of the control (Fig. 1) and B-treated leaves (Fig. 3, advanced symptoms) indicated that mesophyll cells decreased in volume which resulted in an increase of intercellular spaces. Furthermore, mesophyll damage

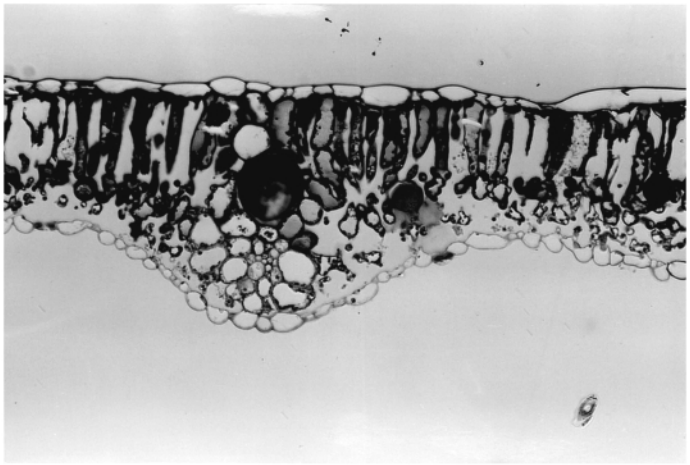

Figure 2. Cross sections (X200) of *Actinidia deliciosa* leaves (early symptoms of boron toxicity, 500 μM).

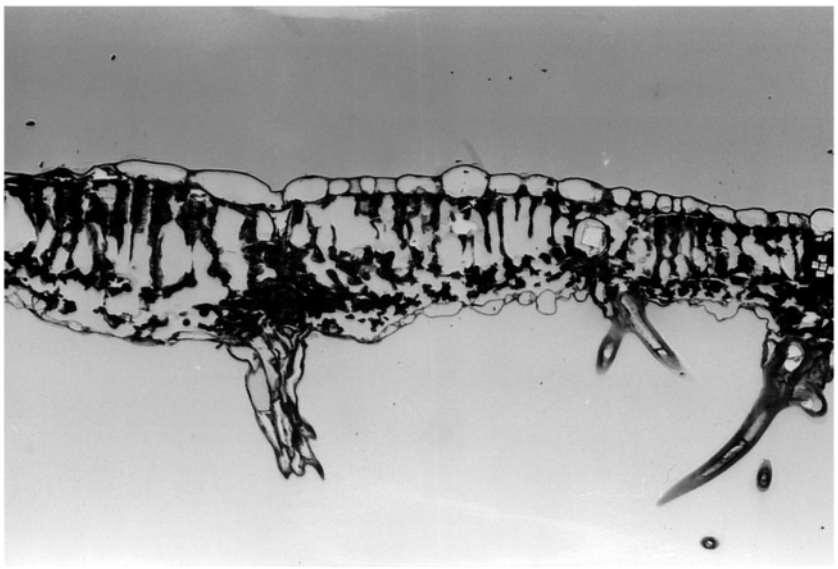

Figure 3. Cross sections (X200) of *Actinidia deliciosa* leaves (advanced symptoms of boron toxicity, 500 μM).

was obvious in B-treated plants. However, epidermal cells were not affected by B toxicity.

Leaf Ion Concentration

Boron was distributed unevenly within leaf parts of both *Actinidia* species. The maximum B concentration was recorded in the leaf margin, while the minimum concentration was recorded in the petioles (Table 3). In the remaining part of the leaf blade, B concentration had intermediate values. By increasing B concentration in the nutrient solution from 20 to 500 μM, its concentration was nearly doubled in the leaf margin and quadrupled in the remaining leaf blade for both *Actinidia* species. The two species did not differ significantly in leaf B concentration and sensitivity to B, as was shown by the results (Table 3).

The highest Ca concentration was recorded in the petioles in comparison to the leaf margin and the remaining part of the leaf blade, for both *Actinidia* species. By increasing B concentration in the nutrient solution from 20 to 500 μM, Ca concentration was decreased in all parts of the leaves of both species (Table 3).

Table 3. The Effect of B Concentration of the Nutrient Solution on Leaf Ion Concentration of Two *Actinidia* Species

Species	Leaf Part	B (μM in Solution)				
		20	50	100	200	500
		B (μg g^{-1} d.w.)				
A. deliciosa	Leaf margin	180 d[+]	199 c	208 b	292 a	298 a
	Remaining leaf blade	42 e	60 d	76 c	91 b	167 a
	Petiole	20 c	22 bc	24 bc	27 ab	32 a
A. arguta	Leaf margin	163 d	200 c	244 b	293 a	301 a
	Remaining leaf blade	49 e	63 d	79 c	101 b	185 a
	Petiole	19 d	20 cd	21 c	25 b	42 a
		Ca (% d.w.)				
A. deliciosa	Leaf margin	2.14 a	1.92 b	1.81 bc	1.72 c	1.70 c
	Remaining leaf blade	1.75 a	1.72 a	1.70 a	1.70 a	1.32 b
	Petiole	2.62 a	2.74 a	2.41 b	2.00 c	1.52 d
A. arguta	Leaf margin	2.10 a	1.97 b	1.91 bc	1.86 c	1.54 d
	Remaining leaf blade	1.81 a	1.80 a	1.56 bc	1.59 b	1.44 c
	Petiole	2.65 b	2.89 a	2.50 c	1.99 d	1.61 e
		Mn (μg g^{-1} d.w.)				
A. deliciosa	Leaf margin	19 b	23 a	18 bc	17 c	12 d
	Remaining leaf blade	21 b	23 a	17 c	17 c	13 d
	Petiole	18 a	17 a	15 b	18 a	14 b
A. arguta	Leaf margin	19 bc	24 a	20 b	18 c	11 d
	Remaining leaf blade	22 b	25 a	19 c	16 d	12 e
	Petiole	19 a	16 b	15 b	18 a	12 c

[+]Means across rows with the same letter are not significantly different at $P \leq 0.05$.

The same trend was also recorded for Mn concentration in the leaf margin and the remaining leaf blade of both *Actinidia* species (Table 3).

Excess B had no significant effect on the concentration of nitrogen (N), P, K, Mg, Fe, and Zn in the leaves of both *Actinidia* species (data not shown).

DISCUSSION

The effect of excess B is a reduction in growth and yield of plants (14). In our experiment, plants of both species produced longer shoots and more leaves per plant with 20 and 50 μM of B in the nutrient solution in comparison to the other treatments. However, plants irrigated with solutions containing 100 μM of B showed a reduction in growth and characteristic B toxicity symptoms (15).

Boron forms borate-ester cross-links with pectin in the cell wall and the breaking and reformation of those borate-ester bonds may control the expansion of cell wall (16). Furthermore, B plays an important role in cell wall structure and plasticity (17). At high concentrations of B (500 μM) the restriction of growth observed was due to the decrease of (Pn) as was shown by the results of the present study and also to a decrease of water use efficiency (4). Furthermore, due to B toxicity, necrotic spots were apparent in the leaf blade. At the end of the experiment the necrotic spots gave a continuous zone of dead tissue between the major veins that had a negative effect on plant's growth.

The two species examined in our experiment did not show statistically significant differences in growth under equal B concentrations. The strong influence of B toxicity on growth parameters of kiwifruit vines is in agreement with other authors (18,19). Similar results were reported in a number of crops including citrus (*Citrus sinensis* L.) (20), pecan (*Carya illinoensis* Wangenh. C. Koch) (21), olive (*Olea europea* L.) (22), and sour cherry (*Prunus cerasus* L.) (23).

The data of the present study indicated that kiwifruit plants are very sensitive to excess B. It is generally accepted that the higher plants do not have an effective mechanism for regulating B uptake (24). Furthermore, because B is carried passively in the transpiration stream, the quantity of B taken up by roots and subsequently transported to the shoots is related to the rate of transpiration (25), which in the case of kiwifruit vines was found to be very high (3). The previous reasons probably account for the intolerance of kiwifruit to comparatively low concentrations of B in the soil solution.

Boron was distributed unevenly within leaf parts, with its highest concentration occurring mostly in the leaf margin, where the mass flow of the transpiration stream ends (25). The accumulation of B in leaf margins and relatively low concentration in roots and shoots (26) indicates that kiwifruit lacks a B exclusion mechanism.

The highest Ca concentration was recorded in petioles. Similar results were obtained for kiwifruit in New Zealand (27). By increasing B concentration in the nutrient solution, Ca and Mn concentrations in leaf parts of both *Actinidia* species were reduced. Our data indicates that B toxicity exerts a strong influence in Ca and Mn absorption and/or transport and does not affect the concentration of the other mineral nutrients.

In our experiment, by increasing B concentration in the nutrient solution the (Pn) of plants decreased. B concentration of 20–50 μM was found to be optimal for the photosynthetic rate of plants. Earlier evidence indicates that B is not directly involved in the photosynthetic process (5,28). Boron deficiency and/or toxicity may indirectly affect photosynthesis by decreasing photosynthetic leaf area and chlorophyll content of leaves (29). The results of the present study suggest that a reduction in growth may occur before the appearance of any symptoms characteristic of B toxicity due to lowered rates of CO_2 fixation and to a loss in leaf area resulting from a reduction in shoot growth. The lower values of (Pn) measured in the present study in comparison to those of kiwifruit plants growing in the field (reaching up to 10 μmol $CO_2\,m^{-2}\,s^{-1}$) (30,31) were probably due to lower light intensity values existent in the growth chamber in comparison to the field.

Stomatal conductance of kiwifruit leaves was not influenced by excess B. Leaves developed under B deficiency had smaller stomatal apertures than those with sufficient B, resulting in a decrease in stomatal conductance to CO_2 (29).

Leaves from kiwifruit plants receiving excess B were characterized by disarranged and shrunken mesophyll cells, accompanied by large conspicuous intercellular spaces. However, epidermal cells were not affected by B toxicity. Similar results were obtained for peach plants grown under B toxicity. Furthermore, B toxicity did not affect the phloem tissue of the leaf but there was a sloughing off of the necrotic ground parenchyma cells along the abaxial side of the leaf midrib (10). Boron deficient sunflower plants produced degenerated chloroplasts and cell walls underwent profound structural changes. Mitochondria increased in number as deficiency developed, while nuclei developed dense rhombohedral structures (9).

Comparison of the effects of B toxicity on leaf anatomy of kiwifruit with those of different crop plants, such as peach (*Prunus persica* L. Batsch) (10) and celery (*Apium graveolens* L.) (32) indicate that the anatomical symptoms are similar, even with these widely different plant species.

Since B toxicity is difficult to overcome and kiwifruit is cultivated as a self-rooted plant in many countries, it is of vital importance to select rootstocks capable to control B absorption and/or transport (4). These mechanisms include: a) the compartmentation of B in root cells and a low B accumulation in leaves, b) the existence of B exclusion mechanisms, c) the existence of different abilities to passively transport B among species, d) the ability of altered

distribution of accumulated B at the cellular, tissue or organ level, e) phloem immobility which keeps B away from key metabolic sites, f) the secretion of B-chelating compounds into the rhizosphere which reduces the amount of free B around the root and g) the existence of genotypic differences of B accumulation governed by differences in transpiration rates and the transport of B in the xylem (2).

The two *Actinidia* species studied did not differ in leaf B accumulation and sensitivity to B. However, a lot of work has to be done in order to select a suitable genotype to be used as a rootstock in order to overcome B toxicity problems.

CONCLUSIONS

The two species examined in our experiment did not show statistically significant differences in growth under equal B concentrations. Plants of both species produced the longest shoots and the greatest shoot fresh weight with 50 μM B in solution. As the B concentration in solution increased from 50 to 500 μM, the shoot length of the two species decreased. B concentration of 20–50 μM was found to be optimal for the photosynthetic rate of kiwifruit plants. B toxicity induced mesophyll damage of leaves but epidermal cells were not affected. By increasing B concentration in the nutrient solution from 20 to 500 μM, its concentration was nearly doubled in the leaf margin and quadrupled in the remaining leaf blade for both *Actinidia* species. The data of the present study indicated that kiwifruit plants are very sensitive to excess B and that the two species did not differ significantly in leaf B concentration and sensitivity to B. By increasing B concentration in the nutrient solution, Ca and Mn concentrations in leaf parts of both *Actinidia* species were reduced. Our data indicates that B toxicity exerts a strong influence in Ca and Mn absorption and/or transport and does not affect the concentration of the other mineral nutrients.

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