Effects of Fertigation Regime on Blossom End Rot of Vegetable Fruits

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Abstract

The relationships between blossom end rot (BER) of vegetable fruits and fertigation regimes are reviewed. Many fruit disorders are affected by nutrient deficiencies or unbalanced nutrition: BER, gold specks, green back, blotchy ripening, color spots, malformation, hollowness, and fruit cracking. Numerous studies have shown that BER is a mineral disorder and that its occurrence could be reduced by improving the supply of specific nutrients. The sensitivity of vegetable fruits to BER varies greatly among cultivars, environmental conditions and fertigation regimes. Some interactions between environmental conditions and fertigation regime are presented. The relation between BER and Ca nutrition is described and discussed in detail. The possibility that Mn may also play a role in the development of BER is discussed.

Keywords: blossom end rot, calcium, magnesium, manganese, oxidative stress, potassium.

Introduction

The aim of the present mini-review is to describe the relationships between blossom end rot (BER) of vegetable fruits and the fertigation regime. Blossom end rot is one of the main mineral disorders affecting tomato and pepper fruits; it reduces marketable yield, especially during hot and dry seasons, by up to 50% (Roorda van Eysinga and van der Meijs, 1981; Winsor and Adams, 1987). More than 50 papers that deal with this disorder have been published in the last 5 years in scientific journals cited by the ISI. Environmental and management factors that enhance or reduce the occurrence of BER are well known and are being studied. During over 60 years of research, BER occurrence has been related to calcium deficiency in the fruit and in the defective tissue; it has been related to reduced translocation of calcium to the fruit tip under stress conditions, and is therefore referred to as a “calcium-related disorder” (Ho *et al.*, 1993; Ho and White, 2005; Marcelis and Ho, 1999). The majority of studies have identified a localized Ca deficiency in the distal fruit tissue as the primary cause of BER (Ho and White, 2005). However, in many studies no correlation was found between BER and Ca concentration in the fruit. On the basis of a thorough review of the literature, Saure (2001) concluded that calcium deficiency per se may not be the only detrimental factor, and that additional "metabolic stress factors" might be involved. In the present paper we will describe observations that support this concept, others that question it, new ideas on the mechanism of BER, and what information is required to advance our understanding of this disorder.

Calcium uptake and translocation

Most soils, except very acidic ones, contain high Calcium concentrations. The Ca concentration in the soil is usually 10 times that of K, but the uptake of the former is usually lower (Kirkby and Pilbeam, 1984). Ca is a divalent ion and as the valence of ion increases the uptake decreases (Marschner, 1995). In contrast to that of K, Ca uptake is limited to the very young section of the roots and the mineral is transported toward the xylem mainly by apoplastic flux, with little translocation in the phloem (Hanson, 1984; Jeschke and Pate, 1991). Calcium deficiency in the fruit may be caused by inadequate Ca uptake, caused, in turn, by low Ca concentration in the solution and by antagonism with other cations (K^+, NH_4^+) (Wilcox *et al*., 1973; Marti and Mills, 1991; Bar-Tal and Pressman, 1996; Bar-Tal *et al*., 2001b, c; Ho and White, 2005). The major pathway for Ca supply to the fruits is by direct transport from the roots via the xylem (Wiersum, 1966; Chiu and Bould, 1976; Ho *et al*., 1993). Calcium uptake and transport in the plant is strongly dependent on transpiration, therefore, the Ca concentration in transpiring organs such as leaves is higher than that in non-transpiring organs such as flowers and fruits (Clarkson, 1984; Hanson, 1984). The main cause for Ca deficiency in fruit is its low mobility in the plant from matured tissues to young ones (Ho and White, 2005; Saure, 2005).

Solution Composition Effects

Ca, K, Mg and NH_4

Numerous studies have shown that BER in tomato fruits can be induced by low Ca (*e.g.*: Maynard *et al*., 1957; Adams and Holder, 1992; Chiu and Bould, 1976; de Kreij, 1996; Taylor *et al*., 2004). We found that increasing the Ca concentration in the irrigation water was an effective means to reduce the incidence of BER in pepper fruits (Table 1), and that it enhanced the Ca content in pepper fruitlets (Table 2).

Table 1. BER occurrence (%) in pepper fruits as affected by three solution Ca concentrations and three irrigation frequencies (after Bar-Tal *et al*., 2001d).

Irrigation frequency	C_{Ca} (ppm)			
(day^{-1})	50	100	150	Mean
	------------------------- % -------------------------			
3	40	37	33	37a
6	44	40	39	41a
12	37	27	32	32b
Mean	40a	35b	35b	

P(f)Ca = 0.018, P(f)irrigation >0.001, P(f)irrigation*Ca = >0.1

Calcium deficiency in plants grown in sufficient Ca levels results mainly from inadequate distribution in the plant organs (Wiersum, 1966; Clarkson, 1984; Ho *et al*., 1987, 1993; Marcelis and Ho, 1999). Therefore, it has been suggested that spraying Ca salts directly onto the fruitlets could be an effective means to eliminate BER. Ho and White (2005) obtained a reduction in the incidence of BER in tomato fruits by spraying the fruitlets with Ca solution, and similar results were obtained by other researchers.

Table 2. Ca concentration in fruitlets (mg/g) as affected by three solution Ca concentrations and three irrigation frequencies (after Bar-Tal *et al*. 2001d).

Irrigation frequency	C_{Ca} (ppm)			
(day^{-1})	50	100	150	Mean
	------------------------- *mg/g* -------------------------			
3	1.58	1.85	1.91	1.78b
6	1.73	2.00	2.17	1.97a
12	1.94	1.99	2.03	1.99a
Mean	1.75b	1.95a	2.04a	

P(f)Ca = 0.001, P(f)irrigation >0.1, P(f)irrigation*Ca = >0.1

The composition of the soil solution may influence plant Ca uptake, because of antagonism with other cations, mainly K^+, Mg^{2+} and NH_4^+. Bar-Tal *et al.* (2001a) reported that increasing the Ca concentration from 0.5 to 4.0 mmol/L resulted in a significant increase in Ca concentrations in the leaves and petals of three rose cultivars. By using K and Mg as the compensating cations, instead of Na, they reduced Ca concentrations in the leaves and petals of the flowering stem of rose (Bar-Tal *et al.*, 2001a).

Use of a high K/Ca ratio in fertilizing tomato plants has been reported to increase the proportion of tomato fruits showing BER (van der Boon, 1973; Taylor *et al.*, 2004). Bar-Tal and Pressman (1996) found that the occurrence of BER increased steeply, from 6.8 to 25.5% when they increased the potassium concentration in a hydroponic system from 2.5 to 10.0 $mmol_c$/L at constant Ca concentration, whereas elevating the Ca concentration from 3.0 to 7.0 $mmol_c$/L reduced the occurrence of BER from 13.7 to 3.3% (Table 3). Increasing the K concentration from 2.5 to 10 mmol/L increased the K concentration in plant organs and the K uptake rate, but reduced that of Ca. However, Bar-Tal and Pressman (1996) found very poor correlations among the incidence of BER, the concentrations of Ca and K, and the K/Ca ratio, in ripe fruits, whereas, they found high correlation between the incidence of BER and the K/Ca ratio in the leaves.

Table 3. Effects of Ca and K concentration on the incidence of BER affected tomato fruits (number of fruits per plant) (after Bar-Tal and Pressman, 1996).

C_K	C_{Ca}	C_K/C_{Ca}	BER	Total
--------- *$mmol_c$/L* ---------			*Number of fruits per plant*	
2.5	3.0	0.83	5.7	83.9
5.0	3.0	1.67	11.3	82.7
10.0	3.0	3.33	22.9	89.8
5.0	7.0	0.71	2.8	84.7
$LSD_{0.05}$			8.0	12.0

Ca and Mg are both alkaline earth elements that are taken up by plants as divalent cations. Schwartz and Bar-Yosef (1983) found that the uptake rate of Ca by young tomato roots decreased as the solution Mg concentration increased. The effect of the Mg concentration on Ca uptake rate was through the value of the rate coefficient (K_m) in the Michaelis-Menten equation, whereas the maximum uptake rate (F_{max}) was not affected. Hao and Papadopoulos (2004) reported an increase in the incidence of BER-affected tomato fruits as the Mg concentration increased from 20 to 80 mg/L when the Ca concentration was 150 mg/L. When the Ca concentration was elevated to 300 mg/L changing the Mg concentration had no effect.

The nitrogen form is an important factor for plant development and yield. Increasing the $N\text{-}NH_4$:$N\text{-}NO_3$ ratio in the N fertilizer reduced the uptake of other mineral cations but increased the uptake of mineral anions by tomato (Kirkby and Mengel, 1967; Ganmore-Neumann and Kafkafi, 1980) and pepper (Marti and Mills, 1991), whereas Sarro *et al.* (1995) reported that ammonium reduced Ca and Mg uptake by pepper, but had no effect on K uptake. Bar-Tal *et al.* (2001c) reported that the uptake of Ca and K increased quadratically as the N-NO_3:$N\text{-}NH_4$ ratio increased, throughout the studied range of 0.25 to 4.0 (Fig. 1).

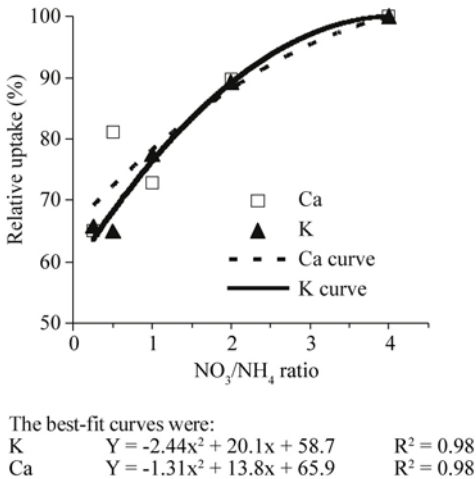

Fig. 1. Effect of NH_4/NO_3 concentrations ratio on K and Ca uptake (after Bar-Tal *et al.*, 2001b).

Blossom-end-rot has been found to be affected by the $N\text{-}NH_4$:$N\text{-}NO_3$ ratio, through its effect on Ca concentration, in the fruits of tomato (Wojciechowski *et al.* 1969; Wilcox *et al.* 1973) and of pepper (Marti and Mills, 1991; Morley *et al.*, 1993). The early stage of fruit development is the period that is most sensitive to Ca supply (Marti and Mills, 1991). Bar-Tal *et al.* (2001b) showed that the occurrence of BER in pepper fruits could be reduced by fertigation in which the nitrogen supply contained a low ammonium fraction (Fig. 2); they found that BER incidence was well correlated with the Ca content in young fruits. The concentration of Ca in mature pepper fruit was three times higher in the distal part of the pepper fruits than in the blossom end, and the effect of the $N\text{-}NO_3$:$N\text{-}NH_4$ ratio on Ca concentration was significant in each part (Bar-Tal *et al*, 2001b). Ho *et al*. (1993) reported that high radiation intensity, combined with NH_4 nutrition, increased the incidence of BER in tomato.

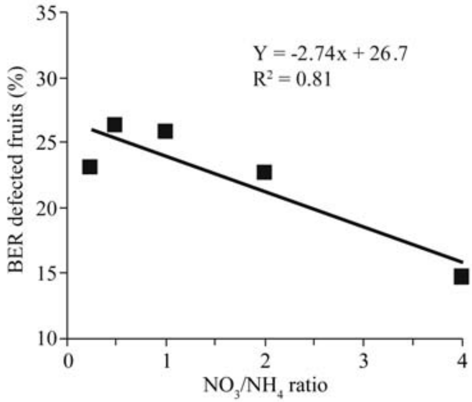

Fig. 2. Effect of NH_4/NO_3 concentration ratio on BER occurrence (after Bar-Tal *et al*. 2001b).

Salinity

Irrigation with saline water enhanced the occurrence of BER in tomato fruits (Ehret and Ho, 1986a; Adams and Ho, 1992; Adams and Holder, 1992). The occurrence of BER in pepper was found to increase dramatically when the EC increased above 1.0 dS/m (Sonneveld, 1979). Aktas *et al*. (2005) and Bar-Tal *et al*. (2003) reported that irrigation with saline solution caused a substantial increase in the percentage of BER-affected fruits, especially when the temperature increased during the spring and summer (Fig. 3).

The increase in the occurrence of BER-affected fruits under irrigation with saline water has been related to reduced Ca uptake and transport into the fruits (Ehret and Ho, 1986a; Adams and Ho, 1992; Adams and Holder, 1992). However, Aktas *et al*. (2005) found that irrigation with saline water that contained high Ca concentration had no effect on the concentration of Ca in BER-free fruits at their initial developmental stage, whereas the calcium concentration in the leaves slightly increased (Table 4). They also found that high salinity caused a substantial decrease in the concentration of manganese in both the fruits and the young leaves (Table 4). This finding led us to investigate the possible role of Mn in the development of BER in fruits.

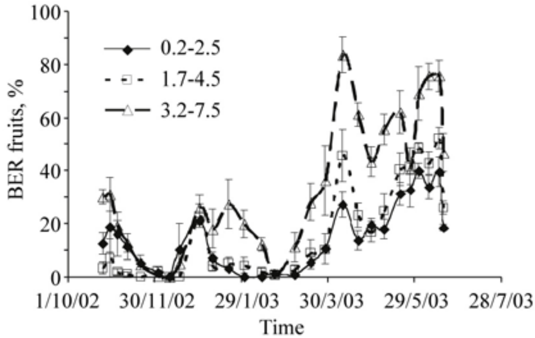

Fig. 3. Effect of salinity on the occurrence of BER (after Aktas *et al*. 2005).

Table 4. The effects of salinity on the dry matter content (DM) and concentrations of Ca and Mn in young fruits and leaves (after Aktas *et al*., 2005).

Salinity level ds/m	1.5		14.5		6.8	
	Fruit	Leaves	Fruit	Leaves	Fruit	Leaves
Dw (%)	4.45		4.87		5.34	
Ca (mg/g)	1.3	19.0	1.3	22.0	1.2	24
Mn (mg/kg)	41.3	283	32.1	214	20.1	61.0

Climate

Several studies have shown that the incidence of BER in tomato is lower under high daytime relative humidity (RH) than under low RH (Adams and Holder, 1992; Adams and Ho, 1993; Brown and Ho, 1993; Ho *et al.*, 1993; de Kreij, 1996; Bertin *et al.*, 2000). However, the opposite effect was found by Banuelos *et al.* (1985), and Tadesse *et al.* (2001) reported that increasing the RH of the air close to the fruit enhanced the incidence of BER in pepper. The effects of air temperature and humidity on BER incidence have been related to their impact on the supply of Ca to the fruit (Wiersum, 1966; Ho, 1989; Brown and Ho, 1993; Ho *et al.* 1993; Ho and White, 2005). It is well accepted that Ca translocation to plant organs is via the xylem, whereas that via the phloem is negligible (Clarkson, 1984; Hanson, 1984). This conclusion is based on measurements of xylem and phloem composition and on the fact that high-transpiring organs contain much more Ca than low-transpiring ones (Hanson, 1984; Baas *et al.*, 2003). Therefore, Ca translocation and distribution in plant are controlled by environmental conditions that affect the transpiration and water status of plant organs (Wiersum, 1966; Brown and Ho, 1993; Ho, 1989; Ho *et al.*, 1993). According to this concept one may expect that, providing that water supply is not a limiting factor, environmental conditions that enhance transpiration would increase the Ca concentration in all organs to the same extent. However, under environmental conditions that enhance transpiration, i.e., low RH and high temperature, the Ca concentration in the leaves increased whereas that in the fruit decreased (Ho, 1989; Adams and Holder, 1992; Ho *et al.*, 1993). This contradiction has been attributed to competition for water between the leaves, which are high-transpiring organs, and the fruits or flowers, which are low-transpiring ones; competition that restricts Ca translocation to the latter (Wiersum, 1966; Ho *et al.*, 1993).

Bar-Tal and Aloni (unpublished data) found that an evaporative cooling system (ECS) and shading reduced the occurrence of BER in pepper fruits during spring and summer (Fig. 4). Bar-Tal *et al.* (2006) found that the effect of the ECS and shading was probably due to reductions in fruit temperature and transpiration, which improved the ability of the plant to maintain the water supply to the fruit through the xylem. However, no consistent effect of the ECS and shading on the Ca concentration in fruit was found.

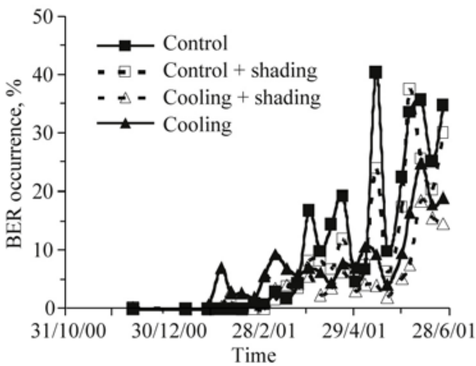

Fig. 4. Effect of evaporative cooling system and shading on the occurrence of BER in pepper fruits.

The use of the ECS reduced the incidence of BER-affected pepper fruits (Bar-Tal *et al*. 2006; Turhan *et al*., 2006b). Bar-Tal *et al*. (2006) reported that the air temperature and the incidence of BER increased with the distance from the wet pad, and high positive correlations were found between the incidence of BER and the average air temperature at midday during the spring. In 3 years of experiments Bar-Tal *et al* (2006) found no clear and consistent effect of the ECS on the Ca concentration in the fruit. Thus, the incidence of BER-affected fruits did not correlate with the Ca concentration in the fruits.

Irrigation frequency and Ca concentration in the solution

The incidence of BER in tomato has been reported to be influenced by the irrigation regime and the quantity of irrigation water (Bangeth, 1979). Bar-Tal *et al* (2001d) reported that the lowest BER incidence was obtained when the most frequent irrigation was combined with the highest solution Ca concentration (Table 1). High irrigation frequency enhanced the Ca concentration in the leaves and fruits, especially in the low-Ca treatment (Table 2), and minimized the amplitude of the fluctuations in the water content of the growth medium, and these effects of the high irrigation frequency probably enhanced the Ca uptake and reduced the BER. In an additional experiment we found that increasing the irrigation frequency in soilless culture from 1 to 12 times a day reduced the percentage of BER-affected pepper fruits from 35 to 25% (Turhan *et al*., 2006b). Silber *et al*. (2005) reported that increasing the fertigation frequency from two to eight and to 30 applications per day reduced the number of BER-affected fruits from 7 to 3 and to 2 per plant, respectively, and increased the yield of export-quality fruits from 6.5 to 10 and to 10.5 per plant, respectively.

The Ca concept

Although the Ca supply to the fruit is considered to be an important factor in the occurrence of BER, many attempts to define critical values or even to correlate BER incidence with the Ca concentration or the K/Ca ratio in tomato and pepper fruits have failed (Chiu and Bould, 1976; Nonami *et al*., 1995; Saure, 2001; Bar-Tal *et al*., 2006). Possible reasons are: i. the fruit is susceptible to the Ca concentration and the K/Ca ratio only during a very short period in early fruit development (Ehert and Ho, 1986b; Ho, 1989; Marti and Mills, 1991; Ho *et al*., 1993; Marcelis and Ho, 1999); and ii. The Ca concentration in the fruit is very low and varies with the distance between the distal part and the blossom end (Ehret and Ho, 1986b; Ho *et al*., 1987; Marcelis and Ho, 1999). The critical Ca concentration for the induction of BER may vary with environmental conditions that affect the fruit growth rate (Ho *et al*., 1993; Marcelis and Ho, 1999). According to Ho and White (2005) BER occurs during a period of high cellular Ca demand, when fruit growth is accelerated or Ca delivery to the fruit is limited; it is initiated by a cellular dysfunction in a fruit cell during expansion, in response to a local, transient Ca-deficiency. During cell expansion, there is a considerable demand for Ca^{2+} as a structural component of new cell walls and membranes, and as a cytosolic signal in the form of a counter-cation in the enlarging vacuole, which orchestrates the allometry and biochemistry of cell expansion. The specific stage of fruit development is crucial, since the Ca concentration in the fruit decreases during fruit growth and ripening (Marcelis and Ho, 1999; Bar-Tal *et al*., 2001b; Ho and White, 2005; Bar-Tal *et al*., 2006; Turhan *et al*., 2006b). Better correlation of the BER incidence with Ca concentration was obtained when analyses of fruit sections were used (Bar-Tal *et al*., 2001b). However, Nonami *et al*. (1995) failed to establish a correlation between BER incidence and Ca concentration in tomato fruits that were divided into several sections. Saure (2001) concluded that stress rather than Ca supply was the main causative factor of BER.

Oxidative stress

However, these stress factors have been neither explored nor identified. Aktas *et al*. (2005) suggested that oxidative stress contributes to BER initiation in bell pepper grown under stress; they reported that BER symptoms were highly enhanced in plants grown in saline conditions during the spring and summer. The fruit calcium concentration was not affected by salinity, but manganese concentrations in both leaves and fruits were significantly reduced under these conditions (Aktas *et al*. 2005). Under salinity reactive oxygen species (ROS) production in the apoplast was enhanced, partly as a result of increased NAD(P)H oxidase activity in the pericarp of pepper fruit at the stage in which it was most sensitive to BER (Aktas *et al*., 2005). Apoplast ROS production and extracted NAD(P)H oxidase activity were inhibited by manganese, zinc and, to a lesser extent, calcium. These cations, especially manganese, also negated the enhancement of ROS production that occurred when fruit pericarp discs were incubated in NaCl solutions (Fig. 5). Manganese, zinc and calcium, when infiltrated into fruit pericarp discs, also inhibited NAD(P)H oxidase activity in extracts. These results suggest that generation and scavenging of oxygen- free radicals in the apoplast may contribute to the appearance of BER symptoms in pepper fruits under saline conditions (Aktas *et al*., 2005). Turhan *et al*. (2006) reported that apoplast-associated peroxidase activity, ascorbic acid, SOD and H_2O_2 may play important roles in controlling salinity-related damage to pepper fruit.

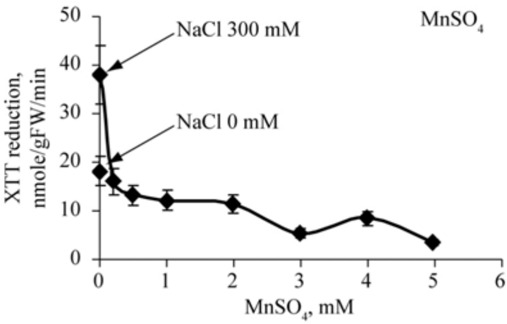

Fig. 5. The effects of Mn on the NaCl-induced enhancement of the XTT reduction rate by fruit pericarp discs (after Aktas *et al*., 2005).

XTT – {2,3-bis(2-methoxy-4-nitro-5-sulfophenyl)-5-[(phenylamino) carbonyl]-2H-tetrazolium hydroxide}.

Does Mn play role in BER occurrence?

Silber *et al*. (2005) reported that Mn concentrations in pepper fruits under low-frequency fertigation were low, probably in the deficiency range, but that they increased with increasing fertigation frequency. During the course of the experiment a negative correlation was found between the accumulated number of BER-affected fruits and the fruit-Mn concentrations (Silber *et al*., 2005). In light of these findings and of the data on the effect of salinity on the incidence of BER-affected fruits (Fig. 3) and on Mn concentration in the fruits (Table 4) we conducted an experiment to investigate the possible effect of Mn concentration on BER incidence in pepper fruits. We found that elevating the Mn concentration in the solution from 0.15 to 1.0 mmol/L dramatically reduced the percentage of BER-affected pepper fruits during the summer (Fig. 6).

Conclusions

BER is a physiological disorder that is influenced strongly by fertigation management and environmental conditions. BER occurrence has been related to reduced translocation of calcium to the fruit tip under stress conditions, and it is, therefore, referred to as a “calcium-related disorder”. In light of recent findings that BER effects in the fruit tissue include the production of oxygen free-radicals and diminution of anti-oxidative compounds and enzymatic activities (Aktas *et al*. 2005; Turhan *et al*. 2006a), and the known crucial role of manganese in enzyme activities and in detoxification of oxygen free-radicals, the relationships between BER incidence and fruit-Mn concentration may indicate that BER is also related to Mn deficiency.

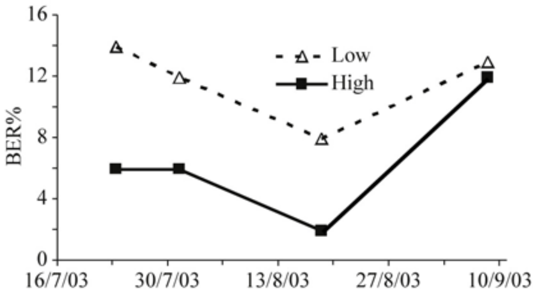

Fig. 6. Effect of Mn concentration in the irrigation water on BER incidence in pepper fruits.

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