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Author(s): P. ADAMS and L.C. HO

Source: *Plant and Soil*, Vol. 154, No. 1, Selected papers from the PROCEEDINGS OF THE EIGHTH INTERNATIONAL COLLOQUIUM FOR THE OPTIMIZATION OF PLANT NUTRITION (July (I) 1993), pp. 127-132
Published by: Springer
Stable URL: http://www.jstor.org/stable/42939009
Accessed: 26-07-2016 22:26 UTC

Plant and Soil **154**: 127–132, 1993.

PLSO IAOPN-223

Effects of environment on the uptake and distribution of calcium in tomato and on the incidence of blossom-end rot

P. ADAMS and L.C. HO
Horticulture Research International, Littlehampton, West Sussex, BN17 6LP, UK

Key words: blossom-end rot, calcium, greenhouse environment, humidity, root-temperature, salinity, tomato, transpiration

Abstract

Studies of Ca uptake and distribution in relation to environmental variables were used to relate Ca status of tomato fruit to blossom-end rot (BER) incidence. Ca uptake was highly correlated with solar radiation and root temperature. The rate of Ca uptake decreased linearly with increasing salinity. High humidity reduced Ca import by the leaves but increased that by the fruit. While total plant dry weight was reduced more than fruit dry weight by salinity, total Ca uptake and the Ca content of the fruit were decreased similarly. Thus, the concentration of calcium in the fruit was substantially reduced by salinity. The distal half of the fruit contained less Ca than the proximal half. The lowest %Ca was found in the distal placenta and locular tissues, where BER first develops. The incidence of BER was often stimulated more by high salinity achieved with the addition of major nutrients than with NaCl. The cause of BER is usually an interaction between the effects of irradiance and ambient temperature on fruit growth and the effects of environmental stress on calcium uptake and distribution within the whole plant.

Introduction

Blossom-end rot is a local deficiency of Ca in tomato fruit. Although this may be caused by dryness or an inadequate supply of Ca in the root zone, it frequently occurs when the moisture and Ca contents of the substrate are fully adequate. In these circumstances, the most likely causes of the disorder are poor Ca uptake by the roots and/or inadequate distribution of Ca to the fruit at a period of high Ca demand.

The uptake of Ca is reduced by osmotic stress (Ehret and Ho, 1986) or by cation competition (Raleigh and Chucka, 1944) in the root zone. As Ca movement in tomato is virtually confined to the xylem, transport of the absorbed Ca to the shoot is either inhibited by high humidity (Adams and Holder, 1992) or salinity (Ho, 1989). While the concentration of Ca in the fruit is intrinsically low (about one tenth of that in the leaves), the transport of Ca within the fruit to the distal half is very poor and is restricted further by high salinity (Ehret and Ho, 1986).

The data reported here show how changes in environmental factors such as light, temperature, humidity and salinity affect both the uptake and distribution of Ca. The tissues most vulnerable to BER are identified from the concentrations of Ca within the fruit.

Materials and methods

The experimental plants were propagated in rockwool cubes, and grown in NFT systems, except where noted otherwise (humidity experiment). A fogging system was used to increase humidity and ventilation to reduce it; all humidity treatments were maintained at the same air temperature (Adams and Holder, 1992). The

actual mean day/night vapour pressure deficits (kPa) achieved were: 0.1/0.1, 0.20/0.15; 0.1/0.8, 0.21/0.45; 0.8/0.1, 0.47/0.16; 0.8/0.8, 0.55/0.50. Increased salinity was achieved by adding NaCl to the basic nutrient solution, except when macronutrients were used for comparison with NaCl (Table 3). Then a mixture of $Ca(NO_3)_2$ and KNO_3 was used that supplied N, K and Ca in the same ratios as in the basic solution. All crops were grown under semi-commercial conditions using the layering system and received solutions containing nutrients within the following concentration ranges (mg L^{-1}): 175–200 N, 30–40 P, 350–400 P, 175–200 Ca, 70–80 Mg, 10–12 Fe, 0.7 – 1.0 Mn, 0.4–0.5 B, 0.4–1.0 Zn, 0.2–0.3 Cu and 0.05–0.1 Mo. The glasshouse atmospheres were enriched with CO_2 to 1000 μL L^{-1} until late April, when frequent venting rendered it impracticable.

Plant material, including fruit, was dried for 48 h at 80°C and ground to pass a 2-mm sieve. The Ca content of the ashed (560°C) material was determined by atomic absorption spectrophotometry. K was estimated by flame photometry.

Results

Responses to light and temperature and humidity

The relationship between water absorption and Ca uptake was investigated using tomato plants grown in NFT. Water uptake during short periods (hours or a day) was closely related to solar radiation over the range 4 to 13 MJ m^{-2} d^{-1} ($r = 0.95$), i.e., water uptake was stimulated as transpiration increased with irradiance. The uptake of Ca was linearly related to that of water ($r = -0.97$; Fig. 1). However, the apparent concentration at which Ca was absorbed decreased from 120 mg L^{-1} to 91 mg L^{-1} as the rate of water uptake increased. Ca uptake also increased with water uptake as the root temperature was increased from 14 to 26°C (Fig. 2). The apparent concentration of Ca absorption was slightly lower at 14 and 26°C (96 and 98 mg L^{-1} respectively) than at 18 and 22°C (both 104 mg L^{-1}). Therefore, Ca uptake can be stimulated by increasing either the root temperature or transpiration rate, but the effects on the ratio of absorbed Ca to water are different.

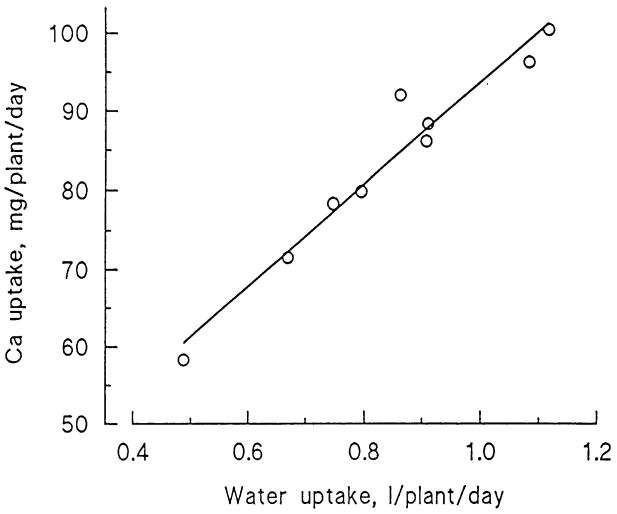

Fig. 1. Relation between the uptakes of Ca and water by fruiting tomato plants grown in NFT. The data represent the relationship for daily irradiances inside the glasshouse over the range 4–13 MJ m^{-2} during September.

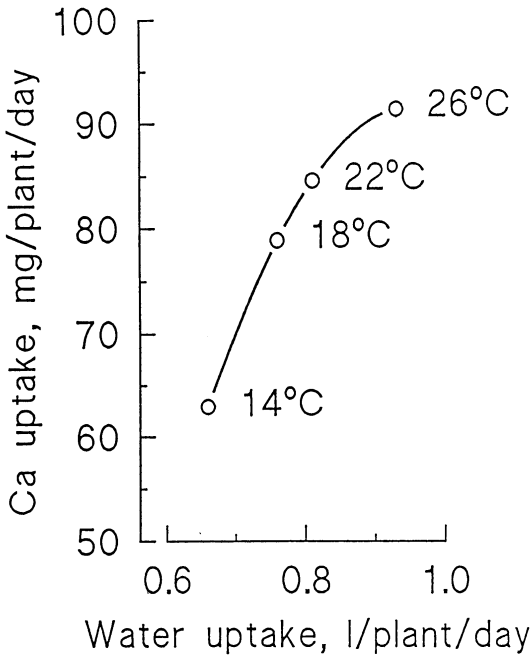

Fig. 2. Effect of root temperature on Ca and water uptake by tomato plants grown in NFT over a period of 10 weeks ending in April.

The distribution of Ca to the leaves and fruit was studied in tomato plants grown in rockwool. Although high humidity restricts Ca distribution to the leaves, the concentration of Ca (%) in the expanding leaves was unaffected by vapour deficits (held constant day and night) in the range 0.15–0.65 kPa. However, as the dry weight of the leaves decreased at high humidity, so did the total amount of Ca accumulated per leaf ($p < 0.01$; Fig. 3). The reduction in leaf size may be related to an inadequate supply of Ca and K, since movement of both nutrients is reduced at high humidity (Adams, 1991). In contrast to the leaves, the %Ca and the total amount of Ca accumulated in the fruit increased with high humidity during the day but was not significantly affected by humidity at night (Table 1). The leaves and fruit therefore respond differently to changes in humidity.

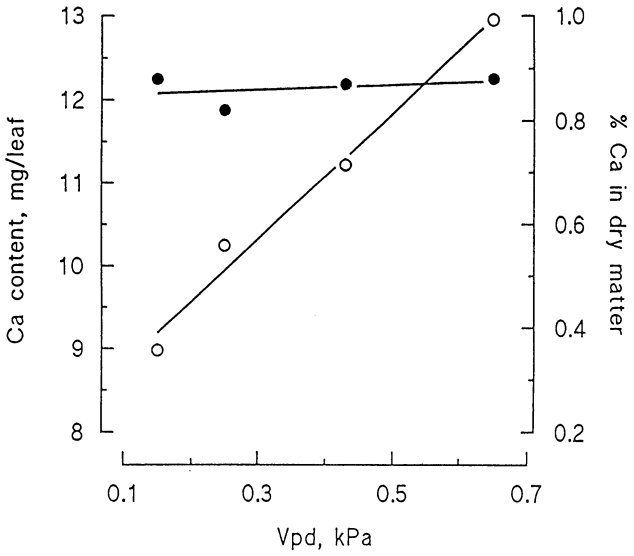

Fig. 3. Relation between the Ca content of tomato leaves in mid-February (fifth below the top) and the ambient vapour pressure deficit, which was held constant throughout the day and night (cv. Counter grown in rockwool). ●, %Ca; o, mg Ca.

Responses to salinity

The effect of salinity on the Ca status of the fruit was studied in conjunction with dry matter partitioning. Increasing salinity reduced the total dry weight per plant and that of the fruit, but increased the proportion of the total dry matter in the fruit (Table 2). The same difference in salinity caused a much greater decrease in Ca uptake and in the %Ca and total Ca content of the fruit, but had little effect on the proportion of the total Ca in the fruit (Table 2). Observations from another experiment showed that the rate of Ca uptake was reduced linearly from 143 mg d^{-1} at 3 mS cm^{-1} to 88 mg d^{-1} at 15 mS cm^{-1} ($r = -0.95$).

Apart from the common osmotic effect, the source of salinity had a considerable influence on the quality and composition of the fruit. A high proportion of the early fruit grown at high salinity (17 mS cm^{-1}) with extra major nutrients developed BER despite the high concentration of Ca in the solution. In contrast, the incidence of BER was negligible when NaCl was used to increase the salinity, even though the concentration of Na in solution was excessive (Table 3). Both sources of salinity increased the acidity of the fruit juices to a high level, but additional K from the added major nutrients stimulated extra acid production; this was evident when the amount of acid per fruit was calculated. Surprisingly, fruit grown with extra major nutrients did not accumulate more Ca than those grown with NaCl, but they had a higher K content. The data suggest a marked antagonism between K and Ca ions affecting Ca uptake whereas Na ions appear to have little effect.

Table 1. Effect of day and night (d/n) humidity on the concentration of Ca (% in dry matter) and on the total Ca content (mg) in young tomato fruit in February (20 d after anthesis; cv. Counter grown in rockwool; sown in October)

	Humidity treatment (d/n), vpd (kPa)				Significance, p	
	0.8/0.8	0.8/0.1	0.1/0.8	0.1/0.1	Day	Night
Ca (%)	0.066	0.066	0.082	0.079	0.001	n.s.
Ca per fruit (mg)	0.89	0.91	1.13	1.04	0.001	(0.07)

Table 2. Effect of salinity on dry matter and Ca accumulation, and on their distribution to the fruit (cv. Counter; sown in January and sampled in April)

	Salinity level (mS cm^{-1})		Significance, p
	5	12	
Total dry matter per plant (g)	165	111	<0.001
Dry matter in fruit (g)	46.7	40.5	n.s.
Total dry matter in fruit (%)	28.3	36.5	<0.001
Ca concentration in whole plant dry matter (%)	1.94	1.52	<0.001
Ca concentration in fruit dry matter (%)	0.91	0.64	<0.001
Total Ca per plant (mg)	3196	1688	<0.001
Ca in fruit (mg)	42.4	25.8	0.003
Total Ca in fruit (%)	1.33	1.53	n.s.

Table 3. Effect of the composition of the nutrient solution on the proportion (%) of harvested fruit with blossom-end rot (BER) and on the chemical composition of the fruit sampled in June (cv. Counter; sown in December). All plants were grown at a constant salinity of 17 mS cm^{-1}, of which the basic nutrient solution contributed 3 mS cm^{-1}

		Salinity source	
		Macronutrients	NaCl
Average nutrient content of solution (mg L^{-1})	Ca	1570	230
	K	5486	420
	Na	120	4500
	Harvest period		
Fruit with BER (%)	April	100	0
	May	94	0.5
	June	9	0
Acidity of fruit	Meq/100 mL juice	12.6	11.4
	Meq/fruit	4.2	2.9
Mineral content of fruit (% in dry matter)	Ca	0.024	0.027
	K	3.27	1.64

The distribution of Ca in tomato fruit

The distribution of Ca between the different tissues of mature green fruit (45-day old) was assessed by dividing them into equal proximal and distal halves. The distal half was then subdivided into two parts, pericarp and placenta. The proximal half had the highest concentration of Ca and 64% of the total Ca content (Table 4). The concentration of Ca was lower in the distal

Table 4. Distribution of Ca in tomato fruit (cv. Counter; sown in December and sampled in May)

	Dry weight per fruit (g)	Total dry weight (%)	Ca (%)	Ca per fruit (mg)	Total Ca (%)
Proximal half (complete)	2.11	50.7	0.208	4.38	63.7
Distal pericarp	1.14	27.4	0.138	1.65	24.0
Distal placenta and associated locular contents contents	0.91	21.9	0.094	0.85	12.4

half than in the proximal half, and was lowest in the distal placenta.

Discussion

The uptake of Ca is determined by root function and transpiration rate. Increasing the root temperature stimulated Ca uptake in proportion to water uptake (Fig. 2) whereas higher transpiration rates increased the rate of water uptake more than that of Ca (Fig. 1). Nevertheless, factors that stimulate water uptake increase Ca uptake.

However, the uptake of Ca does not necessarily determine the Ca status of the fruit, as the accumulation of Ca by fruit is inversely related to the transport of Ca to the leaves. Thus, when leaf size and transpiration were reduced by high humidity, the accumulation of Ca by the leaves was decreased (Fig. 3) while the Ca content of the fruit increased (Table 1). Therefore, in order to meet the requirement of Ca for rapid fruit growth, high rates of transpiration should be avoided. Furthermore, as the uptake of water is much higher during the day than at night, high humidity in the day would increase the Ca status of the fruit more than the same humidity at night. Thus, although the proportion of *newly* absorbed Ca moving into the fruit at night is greater than that during the day, and can be enhanced by high humidity (Ho, 1989), more Ca is absorbed during the day than at night and the increase in Ca in the fruit due to high humidity at night is relatively small.

Salinity reduces Ca uptake mainly by restricting water uptake. However, when the increased salinity is achieved by addition of major nutrients, Ca uptake may be restricted further by competition from K and possibly from Mg (Raleigh and Chucka, 1944). The very high incidence of BER induced when the salinity was increased with major nutrients may have been due to both a low Ca level and a high concentration of free acids in the affected tissues (Table 3). A high concentration of organic acids may reduce the availability of Ca in the tissues and so render the fruit more susceptible to BER. Both the uptake and transport of Ca within the plant (Ehret and Ho, 1986), as well as xylem development inside the fruit (Belda and Ho, 1993) are restricted by high salinity. Hence, salinity has a profound effect on the induction of BER.

The lowest concentration of Ca was found in the distal locular tissue (Table 4) rather than in the distal pericarp, where the external symptom of BER occurs. In fact, the locular tissue is where the earliest symptom appears, before it extends into the placenta (internal BER), or to the blossom-end pericarp (external BER; Adams and Ho, 1992). Therefore, the concentration of Ca in this tissue during the early stage of development is the best index of the Ca status of the fruit in relation to susceptibility to BER.

In this study, we identified the environmental factors causing BER, and these are summarised in Figure 4. The basic cause of BER is a lack of co-ordination between the transport of assimilates by the phloem and of Ca by the xylem during rapid cell enlargement in the distal

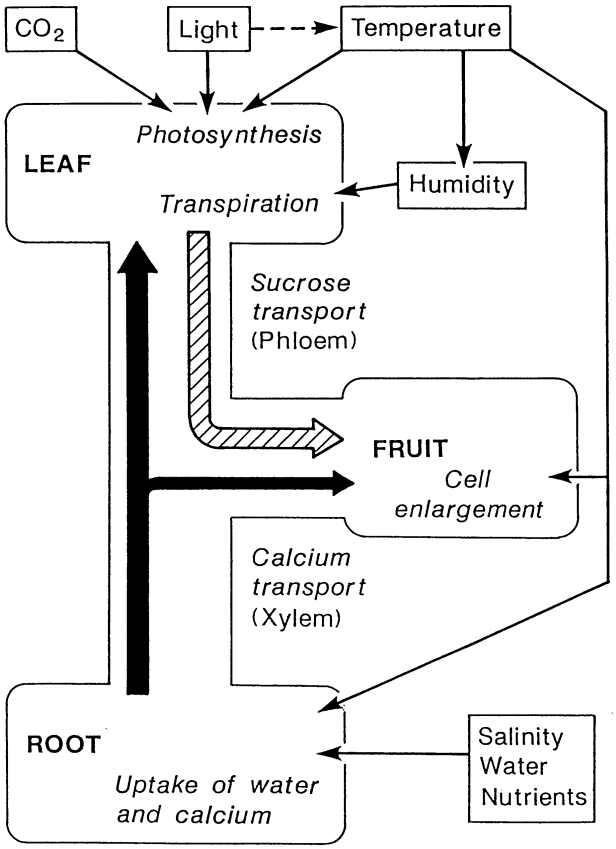

Fig. 4. A summary of factors affecting the uptake and distribution of Ca by tomato plants, and the rate of fruit growth.

placenta tissue, i.e., an interaction between the rates of fruit growth and of Ca acquisition at the distal end of the fruit. Whilst changes in the environment have a marked influence on the incidence of BER, genetic susceptibility is also a major cause of the disorder (Adams and Ho, 1992).

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Section editor: M L van Beusichem