

Blossom-end rot in relation to growth rate and calcium content in fruits of sweet pepper (*Capsicum annuum* L.)

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Abstract

The relative importance of growth rate and calcium concentration in sweet pepper fruits (*Capsicum annuum* L.) for the induction of blossom-end rot (BER) was investigated in (1) four pollination treatments in one cultivar, (2) four cultivars with the same fruit load and (3) three fruit load treatments in four cultivars. For fruits with the same pollination treatment those eventually developing BER had a higher initial fruit growth rate than those not developing BER. Within the same experiment both the growth rate of the young fruit and BER increased with the number of seeds. The Ca concentration of the pericarp in mature fruits was negatively related to both fruit size and BER incidence. Differences in levels of BER between different pollination experiments could not be explained solely by differences in growth rate of the young fruit, but related to different Ca concentrations in the mature fruits. In the spring, but not in the summer, cultivars more susceptible to BER had a larger final size but lower Ca concentration in the young fruit than the resistant ones. By lowering the fruit load in the summer both the final fruit size and the BER incidence increased, but the Ca concentrations of both proximal and distal pericarp in the young fruit of all cultivars were not consistently affected. Despite a correlation between growth rate and low Ca concentration in the fruit, the incidence of BER may only be predicted from separate effects of fruit growth and of Ca concentration in the fruit. The data indicated that at a higher growth rate a higher Ca concentration is required to prevent the induction of BER. The usefulness of the total Ca concentration of

the fruit for determining the critical Ca concentration in the induction of BER is discussed.

Key words: *Capsicum annuum* L., sweet pepper, blossom-end rot, calcium, growth rate, pollination, fruit load.

Introduction

Blossom-end rot (BER) in pepper (Morley *et al.*, 1993) as in tomato fruits (Bangerth, 1979) is the symptom of a physiological disorder caused by local calcium (Ca) deficiency during the initial stage of fruit development (first few weeks after anthesis). The first symptoms of BER in pepper are the appearance of small brown necrotic areas of pericarp tissue in the distal half of the fruit. In both tomato and pepper, the Ca concentration reduces from the proximal to the distal tissue of the fruit where the symptom of BER occurs (Morley *et al.*, 1993; Adams and Ho, 1992). Investigations on the cause of BER in tomato show that low Ca status in the whole plant caused by low supply or uptake of Ca, as well as low transport of Ca to the fruit, particularly to the distal fruit tissue, can induce BER, even when the Ca status in the plant is high (Bradfield and Guttridge, 1984; Ho *et al.*, 1995). Although it is widely accepted that a local deficiency of Ca plays an important role in the induction of BER, there are also some claims that Ca deficiency is not the cause of BER as the critical level of Ca for BER induction was not found (Nonami *et al.*, 1995).

The incidence of BER in tomato has also been shown to be markedly affected by light and temperature, independent of the Ca supply to the plant (Ho *et al.*, 1993). It was previously suggested that accelerated growth rate of the fruit may induce BER in tomato (Westerhout,

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1962; Wiersum, 1966). Therefore, it has been proposed that this increase in BER, associated with accelerated growth, is due to an increased demand of Ca for rapid cell enlargement exceeding the supply of Ca to the susceptible fruit tissue (Ho *et al.*, 1993). In several species, including pepper, a negative correlation has been observed between fruit size and Ca concentration (Mix and Marschner, 1976; Perring, 1979; Tromp, 1979), though some studies did not observe such a correlation (Volz *et al.*, 1993; Boselli *et al.*, 1995). Whether the effects of accelerated fruit growth on the induction of BER can be explained by a higher Ca demand or by a decreased Ca concentration due to higher accumulation of dry matter requires clarification.

The aim of this paper was to verify the relative importance of the fruit growth rate and the Ca concentration in fruits of sweet pepper for the induction of BER. Therefore, treatments that affect the growth rate and final size of fruits, such as pollination (Marcelis and Baan Hofman-Eijer, 1997) and fruit load (Wiersum, 1966) were applied, in order to assess the relationship between BER, fruit growth and Ca concentration in the fruit. As there is a wide range of susceptibility to BER among pepper cultivars (Morley *et al.*, 1993), the incidence of BER in four cultivars with known susceptibility to BER was related to their final fruit size and the Ca concentration in the proximal and distal pericarp from rapidly growing fruits.

Materials and methods

Pollination experiments (Expts 1–4)

Sweet pepper plants (*Capsicum annum* L. cv. Mazurka) were grown in either rockwool (Expt. 1) or aerated nutrient solution (Expts 2–4) in glasshouses at Wageningen, The Netherlands. Plants were pruned to one leader stem with side shoots stopped at one leaf. Plant density was 3 plants m⁻². Only one (Expts 1, 2) or two flowers per plant (Expts 3, 4) were used for pollination treatments. A limited number of naturally self-pollinated competing flowers were retained. Four pollination treatments were applied: (1) low pollination: lanolin was applied on the stigma 2 or 3 d before anthesis to minimize pollination, (2) limited pollination: lanolin was applied the day of anthesis to limit pollination, (3) normal pollination: natural self-pollination, and (4) high pollination: hand pollination at anthesis with pollen of the same flower. Four experiments were carried out at different times of the year. Pollination treatments were carried out in May 1994, August 1994, August 1995, and October 1995 in Expts 1–4, respectively. In Expt. 1, four pollination treatments were applied to 56 plants each and the treated fruits were harvested when they were turning red, about 55 d after anthesis. In Expt. 2, four pollination treatments were applied to 24 plants each and the treated fruits were harvested about 26 d after anthesis. In Expt. 3, only low and high pollination treatments were applied to 12 plants each and the treated fruits were harvested about 38 d after anthesis. In Expt. 4, the same pollination treatments were applied to the same plants as used for Expt. 3, but with a different randomization

of the treatments. The fruits were harvested about 42 d after anthesis.

The growth rate of the individual fruits was estimated from measurements of length and circumference at 17 d after anthesis in Expts 2–4 as described by Marcelis and Baan Hofman-Eijer (1995). The seed number was measured at harvest. Fruit samples were dried at 100 °C for at least 2 d. In Expts 3 and 4 the Ca concentration in the pericarp of fruits about 40-d-old was measured as mg Ca g⁻¹ dry matter. For Ca determination, HCl and trichloroacetic acid was added to the dry matter and boiled for 30 min after addition of BaCl₂ and SrCl₂. Ca was measured by atomic absorption spectrophotometry (Varian AA10).

The average leaf numbers below the first fruit were 40, 10, 2, and 18 in Expts 1–4, respectively. The average glasshouse temperature was 24 °C for Expt. 1 and 22 °C for the other experiments. The average outdoor solar radiation was 17.3, 9.3, 12.3, and 4.4 MJ m⁻² d⁻¹ for Expts 1–4, respectively. Thus, the average daily product of temperature and radiation was 416, 203, 272, and 98 °C MJ m⁻² d⁻¹ for Expts 1–4, respectively. The nutrient solution contained (in mM): 21.3 NO₃⁻, 0 NH₄⁺, 1.5 P, 6.5 K, 8.8 Ca, 3.3 Mg, 0.2 Cl, 3.8 SO₄²⁻, 0.045 Fe, 0.012 Mn, 0.0003 Cu, 0.0017 Zn, 0.0005 Mo, and 0.047 B. In the feed the EC was 3 dS m⁻¹ and pH was 5–6.

In Expts 1–4, the treatments were arranged in a randomized block design. In most experiments abortion of fruits resulted in an unbalanced design for treatment effects on fruit characteristics like fruit size and BER. Analysis of variance was carried out using generalized linear models, with binomial distribution for BER and normal distribution for other fruit characteristics. Differences between treatments were tested by the Students' *t*-test ($P \leq 0.05$).

Cultivar and fruit load experiments (Expts 5, 6)

Four cultivars of pepper, two reported to be very susceptible (i.e. Evident and Farulia) and two less susceptible (i.e. Mazurka and Bendigo) to BER (Morley *et al.*, 1993) were sown on 7 January 1994. The plants were grown in rockwool culture in glasshouses at HRI, Littlehampton, UK. The plant density was 2.8 plants m⁻². Plants were trimmed to two leader stems of even strength with side shoots stopped at 1–2 leaves. In Expt. 5, plants were arranged in three blocks with an incomplete Latin Square for four cultivars within each block. In each block, each cultivar had a plot consisting of two rows of 15 plants each. There were 90 plants of each cultivar in total. In the spring, the incidence of BER (of all fruits) and final fruit size (of fruits without BER) were recorded at harvests between April and May. A number of fruits set at April 1 were tagged and then two fruits per plot were harvested 15 d later for measurement of Ca concentration (i.e. mg Ca g⁻¹ dry matter) and fresh weight of the whole fruit. No treatment was applied to limit the fruit number and the total number of fruits formed was similar among cultivars (about 7 fruits per stem). In the summer experiment (Expt. 6), in early June and prior to the start of the fruit load treatments, all the fruits were removed from the plants of the same crop as used in Expt. 5. In each plot, 30 plants were divided into 3 subplots with either low (3 fruits), medium (5 fruits) or high (8 fruits) fruit load per stem (6, 10 and 16 fruits per plant, respectively). The incidence of BER (of all fruits) and the average final fruit size (of fruits without BER) were recorded at a single harvest at the end of July. From each subplot one fruit of 15-d-old (set at 13 June) was separated into three equal parts (top, middle and bottom). The Ca concentrations (mg Ca g⁻¹ dry matter) of the proximal (top third) and the distal (bottom third) pericarp tissue were

measured. Fruit samples were dried in an oven at 80 °C for 3 d and the dry weights were recorded. Ca was determined in the acid extract of the ashed (560 °C) fruit samples by atomic absorption spectrophotometry.

In Expt. 5, the heating temperature setting of the glasshouse was kept 21 °C day and 19 °C night with venting temperature at 26 °C. The average outdoor solar radiation for fruit growing period of Expt. 5 in April and May was 15.7 MJ m⁻² d⁻¹ and that of Expt. 6 in June and July was 27.5 MJ m⁻² d⁻¹. The nutrient solution contained (in mM): 14.8 NO₃, 0.4 NH₄, 1.3 P, 7.7 K, 4.7 Ca, 1.6 Mg, 3.2 Cl, 2.1 SO₄, 0.04 Fe, 0.009 Mn, 0.006 Cu, 0.008 Zn, and 0.05 B. During the fruiting period, the feed was kept at an EC of about 2 dS m⁻¹ and pH 5.

Analyses of variance were carried out to assess effects of cultivars and fruit load on parameters, with a normal distribution, such as BER, fruit size, Ca concentration and Ca content. Students' *t*-test was used to calculate least significant differences (LSD) at *P* ≤ 0.05.

Results

BER in relation to pollination

An increase in pollen load increased BER incidence in most experiments (Fig. 1A). Within the same pollination treatment, i.e. normal or high pollination, initial growth rates of fruits eventually developing BER were higher than those of fruits not developing BER (Table 1). For the pollination treatments which did not induce BER (low pollination) or induced low incidence of BER (limited pollination), the initial fruit growth rates were relatively low and no difference in growth rate was found between fruits developing or not developing BER.

As reported previously the degree of pollination affected both fruit size and number of seeds (Marcelis and Baan Hofman-Eijer, 1997). In all pollination experiments, except Expt. 4 where BER did not occur, the incidence of BER was positively correlated to either the number of seeds at harvest (Fig. 1A) or the initial fruit

Table 1. Initial growth rate of pepper fruits *cv. Mazurka* that eventually did or did not develop BER at four levels of pollen load

Initial growth rate is the average rate (\pm SE_{mean}) of fresh weight increase from 0 until 17 d after anthesis in Expt. 2; between brackets are numbers of replicates.

Pollen load	Fruit growth rate (g d ⁻¹)	
	Non-BER	BER
Low	1.40 ± 0.16 (10)	—
Limited	1.79 ± 0.18 (16)	1.72 ± 0.37 (2)
Normal	1.80 ± 0.17 (17)	2.57 ± 0.20 (7)
High	1.74 ± 0.21 (13)	2.61 ± 0.37 (6)

growth rate during the first 17 d after anthesis, the period just before BER started to develop (Fig. 1B).

Despite a high correlation between BER and seed number or initial fruit growth rate within the same experiment, the levels of BER differed between experiments over similar ranges of seed number or initial fruit growth rate. The occurrence of BER between experiments correlated with the product of average daily temperature and solar radiation (energy sum). For instance, at high pollen load the incidences of BER were 0, 32, 38, and 74%, while the energy sums were 98, 203, 272, and 416 °C MJ m⁻² d⁻¹, for Expts 4, 2, 3, and 1, respectively. Therefore, although the seed number and fruit growth rate were affected by pollination treatments in Expt. 4, no BER was recorded, while the energy sum was the lowest among all experiments.

The different responses to pollination treatments in the incidence of BER between Expts 3 and 4 (Fig. 1) were found to be related to the Ca concentration in the pericarp of fruit of 40-d-old (Fig. 2). While the Ca concentrations in the pericarp with low pollen load treatment were higher than those with high pollen treatment in both experiments,

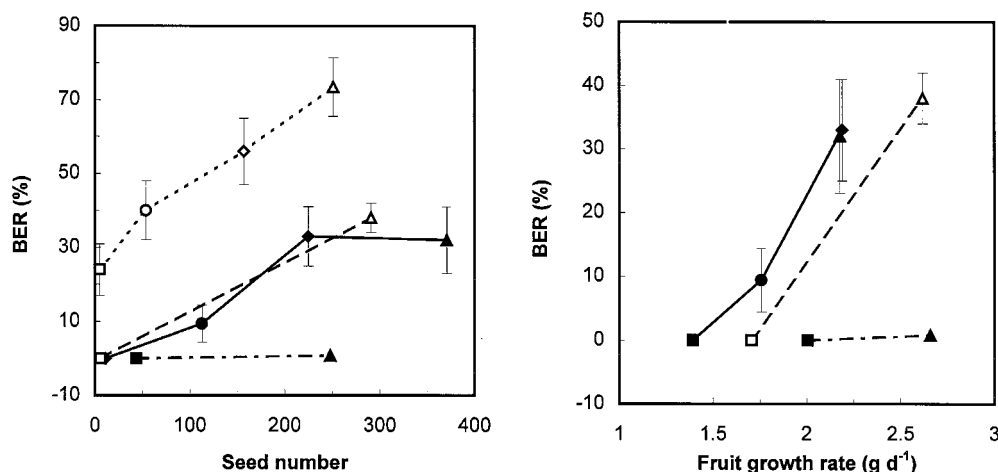


Fig. 1. Relationship between the incidence of BER (number of BER fruits as % of total fruit number) and (A) the seed number or (B) the initial fruit growth rate (from 0–17 d after anthesis) in pepper fruits *cv. Mazurka* manipulated by pollen load, i.e. low (square), limited (circle), normal (diamond), and high load (triangle) in Expts 1 (.....), 2 (—), 3 (---), and 4 (-·-). Bars indicate standard errors of means.

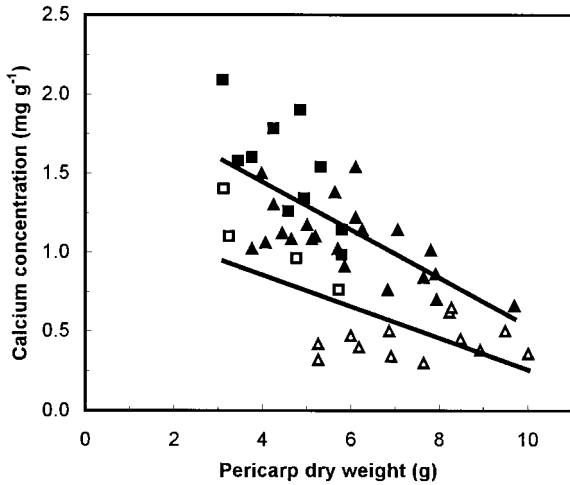


Fig. 2. Relationship between dry weight and Ca concentration in pepper fruits cv. Mazurka about 40-d-old in Expts 3 (open) and 4 (closed) under either low (square) or high (triangle) pollen load. The relationship can be described by $y=1.25-0.100x$; $r^2=0.44$ for Expt. 3 and $y=2.05-0.152x$; $r^2=0.46$ for Expt. 4. Fruits with BER were excluded from the analysis.

the average Ca concentrations in Expt. 3 (1.06 and 0.43 mg g⁻¹ in low and high pollen load, respectively) were lower than those in Expt. 4 (1.52 and 1.07 mg g⁻¹, correspondingly). However, within the same experiment, the total Ca content per fruit (pericarp+seeds) was not significantly affected by pollination treatment. Ca contents in fruits with low and high pollen load were 4.24 and 3.38 mg (LSD=1.45) in Expt. 3 and 6.85 and 6.55 mg (LSD=1.14) in Expt. 4, respectively. As a whole, the Ca concentration was inversely related to the dry weight of the pericarp (Fig. 2). Thus, the increase in the incidence of BER, manipulated by pollination, was associated with an increase in fruit growth rate in the young fruit or with a decrease in Ca concentration in the pericarp of the mature fruit.

BER in relation to cultivar susceptibility and fruit load

Consistent with previous findings (Morley *et al.*, 1993), Fig. 3A showed that the incidence of BER was lower in Bendigo and Mazurka than in Evident and Farulia in the spring (Expt. 5). The cultivar susceptibility to BER was related to the initial fruit growth and Ca concentration in the young fruit. Fifteen days-old fruits were heavier in the more susceptible cultivars, i.e. 46.9 g for Farulia and 24.8 g for Bendigo (Fig. 3B; LSD=9.9). Although there seemed to be a negative correlation between Ca concentration of the whole fruit (Fig. 3C) and BER incidence among cultivars (Fig. 3A), the differences in Ca concentration were not statistically significant.

In contrast to the spring crop, cultivar susceptibility in the summer was highest in Evident (59% BER, averaged over all fruit load treatments) and lowest in Mazurka (22%), with Bendigo (30%) and Farulia (35%) inter-

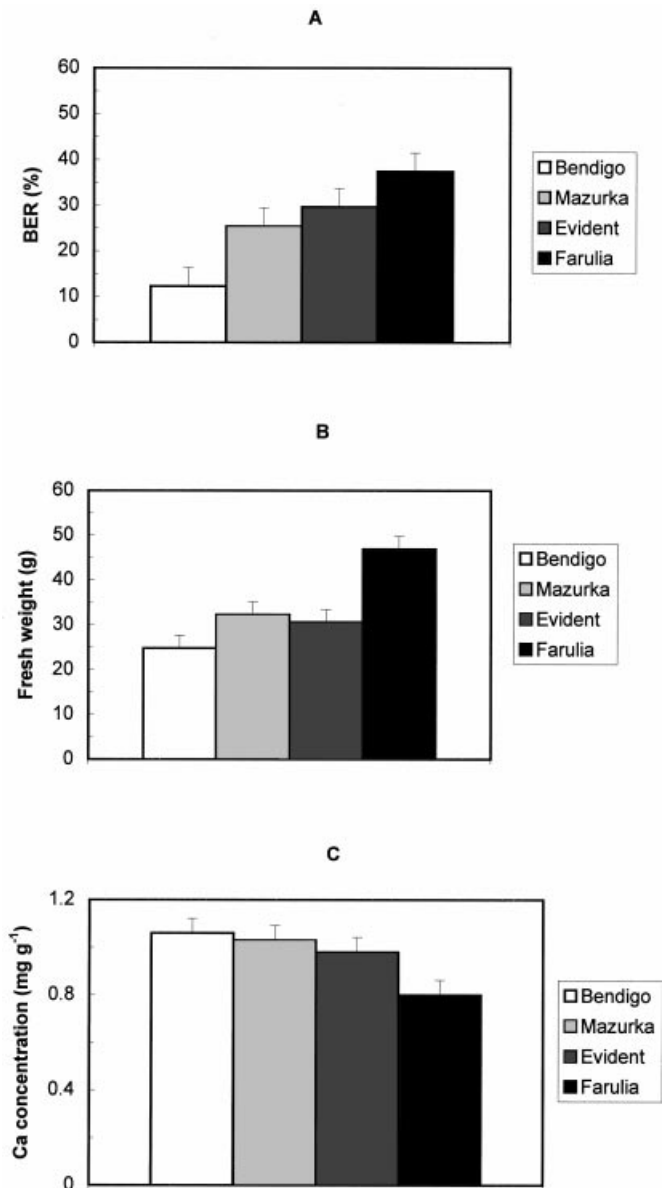


Fig. 3. (A) The incidence of BER (number of BER fruits as % of total fruit number), (B) the fresh weight and (C) the Ca concentration in 15-d-old fruit in four cultivars of pepper, i.e. Bendigo, Mazurka, Evident, and Farulia in the spring experiment (Expt. 5). Bars indicate standard errors of means.

mediate in response (Fig. 4; LSD=11). The cultivar susceptibility in the summer experiment was not consistently related to the differences in final fruit weight (Fig. 4). For instance, although Mazurka had the lowest incidence of BER in all fruit load treatments, their final fruit sizes were either larger or similar to the more susceptible cultivars. In the summer experiment (Expt. 6) the average final fruit size of all cultivars was increased by limiting the fruit load from 8 to 5 and 3 fruits per stem (Fig. 4). Under the low fruit load treatment the final fruit size was 34% or 25% higher than that under high fruit load

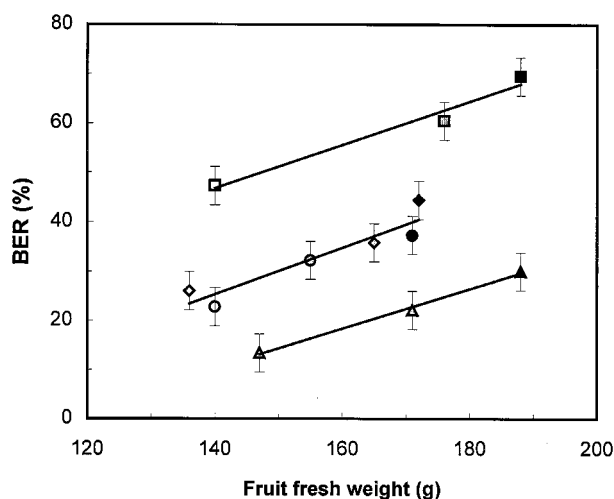


Fig. 4. Relationship between the final weight of healthy fruits and the incidence of BER (number of BER fruits as % of total fruit number) in the four pepper cultivars Bendigo (circle), Mazurka (triangle), Evident (square), and Farulia (diamond) when the fruit load was 3 (closed), 5 (half-filled) and 8 (open) fruits per stem in the summer experiment (Expt. 6). The relationship can be described by $y = -14.9 + 0.44x$ ($r^2 = 0.970$) for Evident, $y = -40.9 + 0.47x$ ($r^2 = 0.878$) for Bendigo and Farulia and $y = -46.0 + 0.40x$ ($r^2 = 0.996$) for Mazurka. Bars indicate standard errors of means.

treatment in Evident or other cultivars, respectively. The increase in fruit size as caused by a decrease in fruit load was positively related to the incidence of BER in each cultivar. The average BER incidences in all cultivars were 27, 38 and 45% for high, medium and low fruit load treatments, respectively (LSD=9.8). BER incidence increased linearly with final fruit size when fruits were pruned, and the increases in BER of $0.40\text{--}0.47\%$ g^{-1} fruit weight were similar among cultivars. The relationship between the incidence of BER and the Ca concentration in the pericarp of fruits about 15-d-old is shown in Fig. 5. The Ca concentrations in the proximal pericarp (ranging from 0.9 to 1.4 mg Ca g^{-1} DM) were higher than those in the distal tissue (ranging from 0.3 to 0.4 mg Ca g^{-1} DM) of the same fruit. The most susceptible cultivar had the lowest and the least susceptible one the highest Ca concentration in the distal tissue. In addition, the more susceptible cultivars had lower Ca concentrations (ranging from 0.9 to 1.2 mg Ca g^{-1} DM) than the less susceptible ones (ranging from 1.2 to 1.4 mg Ca g^{-1} DM) in the proximal tissue. However, the Ca concentration in the pericarp tissue was not reduced by low fruit load consistently, despite the increase in BER by low fruit load in all cultivars. Multiple regression analysis showed that 62% of the variation in BER observed in the summer experiment could be explained by variation in final fruit fresh weight (FW in g of healthy fruits) and Ca concentration in the distal fruit parts (mg Ca g^{-1} DM) of about 15-d-old fruits ($\%BER = 5 + 0.72FW - 243Ca$). This analysis showed that BER incidence correlated significantly with

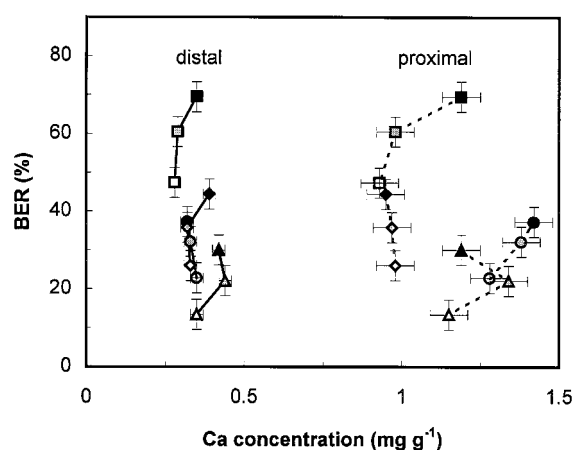


Fig. 5. Relationship between the Ca concentration in either the proximal (broken lines) or distal (solid lines) pericarp of fruit about 15-d-old and the incidence of BER in four pepper cultivars in Expt. 6. Symbols are the same as in Fig. 4.

both fruit size and Ca concentration independent from each other.

Discussion

BER in pepper became visible from about 3 weeks after anthesis. Over this period both the rate of fresh weight and dry weight gain in pepper fruit increased rapidly and reached the maximum rate (Marcelis and Baan Hofman-Eijer, 1995). This rapid initial growth can be increased further by a high pollen load (Marcelis and Baan Hofman-Eijer, 1997). In accordance with observations of Morley (1996), the initial rapid fruit growth appeared to play an important role in the induction of BER in pepper fruits. In tomato, the induction of BER coincided with a low Ca concentration during the period of rapid growth (Ehret and Ho, 1986). In the present pollination experiments with pepper, a positive relationship between fruit size and BER and a negative relationship between fruit size and Ca concentration (Figs 1, 2; Table 1) was observed. This negative correlation may be explained in terms of an increase in phloem transport of assimilates without an increase in xylem transport of Ca during accelerated fruit growth. The gain of dry matter and water in the tomato fruit is mainly supplied by phloem transport, while the accumulation of Ca is limited by xylem transport (Ho *et al.*, 1987). Hence, an imbalance between transport of assimilates and Ca during accelerated growth could be the common cause of the induction of BER in tomato and pepper. However, accelerated fruit growth did not always lead to a reduction in the Ca concentration of the fruit. For instance, in our fruit load experiment the Ca concentration in the pericarp (Fig. 5) was unaffected by fruit load despite a strong effect on fruit size (Fig. 4), which is in contrast with the observation by Mix and Marschner (1976). As an enhanced

import of assimilates may be accompanied by enhanced import of K, the cause of BER may not be entirely due to a low Ca concentration but to a high K/Ca ratio in the fruit tissue as reported in tomato (Wiersum, 1966; Ho, 1980).

Most of the observations in this study showed a positive correlation between the incidence of BER and growth rate or fruit size, except that (a) no BER was observed in Expt. 4 while the fruit growth rates were similar to those in Expt. 3 under similar pollination treatments (Fig. 1B), and (b) the final fruit size of four cultivars did not correspond to their cultivar susceptibility of BER (Fig. 4). However, in both cases BER incidence was negatively related to Ca concentration in the fruit tissues (Figs 2, 5). Similarly, most observations showed a positive correlation between the incidence of BER and a low Ca concentration, except that the enhanced BER incidence by fruit load cannot be explained by a reduction of Ca concentration in the distal pericarp tissue (Fig. 5). However, as revealed by the multiple regression analysis, the induction of BER can be explained by two independent effects of fruit growth rate and Ca concentration. Our findings support previous suggestions that the Ca demand for fruit tissue development increases when growth accelerates which may cause local Ca deficiency (Ho *et al.*, 1993). Hence, the observations indicate that the critical Ca concentration for the induction of BER may decrease with increasing growth rate.

Similar to observations in tomato (Ho *et al.*, 1993), the incidence of BER in pepper showed a positive correlation with the product of temperature and radiation. Furthermore, the change of BER susceptibility among cultivars from spring to summer may be influenced by the higher temperature sensitivity in Bendigo and Evident than in Mazurka and Farulia (Figs 3, 4). Apart from the effects of temperature and radiation, leaf area and number of competing fruits on the plant may also affect the growth rate of the individual fruits. It may explain why in the experiment with the least radiation (Expt. 4) the fruit growth rate was not the lowest. Apart from affecting the fruit growth rate, higher temperature and radiation may reduce Ca import into a fruit by increasing crop transpiration which enhances the fraction of Ca transported to the leaves (Mix and Marschner, 1976; Aikman and Houter, 1990). Thus, any increase in temperature and radiation is likely to increase the assimilate import, but to decrease the Ca import into the fruit, leading to an increased incidence of BER.

It has long been recognized that the Ca concentration in the distal placental tissue of the fruit during the rapid expansion period, rather than the Ca concentration of the whole fruit at maturity, is critical for the induction of BER in tomato (Ehret and Ho, 1986; Adams and Ho, 1992). The negative relationship between Ca concentration of the whole fruit and the incidence of BER revealed

by the pollination (Fig. 2) and cultivar experiments (Fig. 3) in this investigation supports the suggestion that BER in sweet pepper is also caused by Ca deficiency. Furthermore, the Ca concentration of the distal pericarp tissue was found to be negatively correlated with the cultivar susceptibility and was much lower than those in the proximal pericarp tissue (Fig. 5). However, the lack of relationship between the BER incidence and the Ca concentration in the distal pericarp tissue in the fruit load experiment is likely explained by the fact that the critical Ca concentration should be the concentration of Ca relevant to the membrane permeability rather than the total Ca concentration which is dominated by free Ca in the extracellular pool and Ca oxalate in the vacuole (Minamide and Ho, 1993). Therefore, measurements on the concentrations of individual Ca compounds at the subcellular level in the distal pericarp are essential in future work to quantify the critical Ca concentration for the induction of BER.

The findings in this investigation have provided some useful pointers for the prevention of BER in pepper. Firstly, providing that the supply of Ca is adequate, the incidence of BER may be reduced by avoiding accelerated fruit expansion caused by high assimilate import. In practice, partial shading during the high summer (to avoid too much import of assimilate by the rapidly growing fruit) and frequent picking to maintain an even fruit load are effective to balance the supply and demand for Ca in individual fruits during rapid fruit growth. Secondly, bee pollination should not be used for the large-fruited cultivars or at conditions that favour rapid fruit growth. The benefit of good pollination in producing larger fruits may likely be nullified by the yield loss caused by BER.

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References

- Aikman DP, Houter G. 1990. Influence of radiation and humidity on transpiration: implications for calcium levels in tomato leaves. *Journal of Horticultural Science* **65**, 245–253.
- Adams P, Ho LC. 1992. The susceptibility of modern tomato cultivars to blossom-end rot in relation to salinity. *Journal of Horticultural Science* **67**, 827–839.
- Bangerth F. 1979. Calcium-related physiological disorders of plants. *Annual Review of Phytopathology* **17**, 97–122.
- Boselli M, Volpe B, Di Vaio C. 1995. Effect of seed number per berry on mineral composition of grapevine (*Vitis vinifera* L.) berries. *Journal of Horticultural Science* **70**, 509–515.

- Bradfield EG, Guttridge CG.** 1984. Effects of night-time humidity and nutrient solution concentration on the calcium content of tomato fruit. *Scientia Horticulturae* **22**, 207–374.
- Ehret DL, Ho LC.** 1986. Translocation of calcium in relation to tomato fruit growth. *Annals of Botany* **58**, 679–688.
- Ho LC.** 1980. Control of import into tomato fruits. *Berichte der Deutschen Botanischen Gesellschaft* **93**, 315–325.
- Ho LC, Grange RI, Picken AJ.** 1987. An analysis of the accumulation of water and dry matter in tomato fruit. *Plant, Cell and Environment* **10**, 157–162.
- Ho LC, Belda R, Brown M, Andrews J, Adams P.** 1993. Uptake and transport of calcium and the possible causes of blossom-end rot in tomato. *Journal of Experimental Botany* **44**, 509–518.
- Ho LC, Adams P, Li XZ, Shen H, Andrews J, Xu ZH.** 1995. Responses of Ca-efficient and Ca-inefficient tomato cultivars to salinity in plant growth, calcium accumulation and blossom-end rot. *Journal of Horticultural Science* **70**, 909–918.
- Marcelis LFM, Baan Hofman-Eijer LR.** 1995. Growth analysis of sweet pepper fruits (*Capsicum annuum* L.). *Acta Horticulturae* **412**, 470–478.
- Marcelis LFM, Baan Hofman-Eijer LR.** 1997. Effects of seed number on competition and dominance among fruits in *Capsicum annuum* L. *Annals of Botany* **79**, 687–693.
- Minamide RT, Ho LC.** 1993. Deposition of calcium compounds in tomato fruit in relation to calcium transport. *Journal of Horticultural Science* **68**, 755–762.
- Mix GP, Marschner H.** 1976. Einfluss exogener und endogener Faktoren auf den Calciumgehalt von Paprika- und Bohnenfrüchten. *Zeitschrift für Pflanzenernaehrung und Bodenkunde* **5**, 551–563.
- Morley PS.** 1996. Calcium nutrition and the physiology of sweet pepper (*Capsicum annuum* L.) fruit. PhD thesis, Leeds University, UK.
- Morley PS, Hardgrave M, Bradley M, Pilbeam DJ.** 1993. Susceptibility of sweet pepper (*Capsicum annuum* L.) cultivars in the calcium deficiency disorder ‘blossom-end rot’. In: Frago MAC, Van Beusichem ML, eds. Optimization of plant nutrition. The Netherlands: Kluwer Academic Publishers, 561–567.
- Nonami H, Fukuyama T, Yamamoto M, Yang L, Hashimoto, Y.** 1995. Blossom-end rot of tomato plants may not be directly caused by calcium deficiency. *Acta Horticulturae* **396**, 107–114.
- Perring MA.** 1979. The effects of environment and cultural practices on calcium concentration in the apple fruit. *Communications in Soil Science and Plant Analysis* **10**, 279–293.
- Tromp J.** 1979. The intake curve for calcium into apple fruits under various environmental conditions. *Communications in Soil Science and Plant Analysis* **10**, 325–335.
- Volz RK, Ferguson IB, Bowen JH, Watkins CB.** 1993. Crop load effects on fruit mineral nutrition, maturity, fruiting and tree growth of ‘Cox’s Orange Pippin’ apple. *Journal of Horticultural Science* **68**, 127–137.
- Westerhout J.** 1962. Relation of fruit development to the incidence of blossom-end rot of tomatoes. *Netherlands Journal of Agricultural Science* **10**, 223–234.
- Wiersum LK.** 1966. Calcium content of fruits and storage tissues in relation to the mode of water supply. *Acta Botanica Neerlandica* **15**, 406–418.