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# Plant Nutrition and Physiological Disorders in Greenhouse Grown Tomato, Pepper and Eggplant

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## ABSTRACT

Optimization of the nutritional status of plants is fundamental to high production in a greenhouse environment, and especially so in the case of fast-growing, high-yielding Solanaceous vegetables such as tomato, pepper and eggplant. Nutritional disorders (deficiencies and toxicities) may arise in either soil or soilless media due to imbalanced fertilization and/or shortcomings in the root environment and can result in serious losses of yield and quality. The present paper reviews research findings related to the nutrition of greenhouse Solanaceous vegetable crops when cultivated in the soil or in hydroponic systems. In addition, some of the more frequently observed physiological disorders, particularly those affecting fruit quality and to a significant extent resulting from nutritional and/or environmental deficiencies are reviewed. The scope of the review is to summarize our current knowledge concerning plant nutrition management in soil- and soilless-grown tomato, pepper and eggplant crops as well as the impact of nutrition and greenhouse environment on the main physiological disorders of these crops.

**Keywords:** *Capsicum annuum*, fertilizers, fruit quality, *Lycopersicon esculentum*, plant nutrients, physiological disorders, soilless culture, *Solanum melongena*

**Abbreviations: BER**, blossom-end rot; **EC**, electrical conductivity; **EU**, European Union; **IFR**, internal fruit rot; **NFT**, nutrient film technique; **TMV**, tobacco mosaic virus; **YSD**, yellow shoulder disorder; **VPD**, vapour pressure deficit

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**Invited Review**

## INTRODUCTION

Plant growth and development is closely associated with the crop environment and the nutrient supply, which in turn affects the yield and quality of the produce. For intensive vegetable production in greenhouses (Heuvelink 2005), an understanding of the impact of the greenhouse environment and nutrient supply on the physiological processes of growth and development is particularly important in order to achieve high yields and quality; as a consequence, an appreciable number of studies have focused on this theme (Papadopoulos and Hao 2002). The impact of the greenhouse environment is discussed in a parallel review by Katsoulas and Kittas (2008), whereas here the role of plant nutrition is presented together with a discussion of disorders that primarily affect the quality of produce and are caused by nutritional and/or environmental factors.

## NUTRITION OF SOIL-GROWN SOLANACEOUS CROPS

### Introduction

Within the greenhouse, cultivation is carried out under environmental conditions that are controlled to a greater or lesser extent depending on the type of greenhouse structure, the level of technological input and the crop management expertise. Plant nutrition is a crop management factor with a pronounced effect on both the yield and quality of greenhouse vegetable crops, such as tomato (*Lycopersicon esculentum* Mill.), pepper (*Capsicum annuum* L.) and eggplant (*Solanum melongena* L.). Therefore, knowledge of the specific nutrient requirements of these crops in relation to plant growth and the greenhouse environment is of major importance in the search for more efficient nutrient management, enhanced fruit yield and improved product quality. Many effects of inorganic nutrition on fruit quality of the greenhouse Solanaceae are associated with the occurrence of physiological disorders. In soil-grown greenhouse crops, part of the nutrients required by the plants is applied as a base-dressing. This is particularly the case with P (Sonneveld 1995), which is rather immobile in the soil. In contrast, N, which is highly soluble in water in the form of both nitrate and ammonium salts, and as a result easily leaches out of the root zone, is applied after planting through the irrigation system. In modern greenhouse cultivation systems, not only N but also K and perhaps some other nutrients (e.g. Mg, micronutrients) may be applied to the crop by dissolving water soluble fertilizers in the irrigation water. This operation, which is widely known as fertigation, saves time, labour, and resources, while maintaining or even improving crop yields (Bar Yosef 1999). Appropriate type, amount and time of nutrient applications considerably increase water use efficiency. The use of suitable dosing pumps or injectors enabling the maintenance of optimal nutrient concentrations in the irrigation water applied to a crop is a prerequisite for balanced plant nutrition even in soil-grown greenhouse crops. The optimum nutrient concentrations for each crop need to be adjusted.

### Tomato

Greenhouse tomato is characterized by high nutrient requirements owing to rapid growth rates and heavy fruit loads (Chapagain and Wiesman 2004). In an experiment conducted in the U.K., the daily N, P and K uptake of a tomato plant bearing fruits ranged from 90-130 mg, 25-30 mg, and 150-320 mg, respectively (Adams 1993). According to Sonneveld (2002), the total N uptake by a long-term tomato crop yielding approximately 60 kg $m^{-2}$ was estimated to be about 1185 kg $ha^{-1}$. These figures may be used to roughly estimate the total nutrient requirements of a tomato crop taking into consideration the plant density, the duration of growth and the utilization coefficient of each particular nutrient when it is applied to the soil. However, these values may be higher under Mediterranean growing conditions (Savvas and Ntatsi, unpublished data). Furthermore, it should be taken into consideration that the nutrient uptake requirements are much smaller at an early vegetative growth stage, when the plant size is still small. Indeed, at the early growth stage (1$^{st}$ flower truss) the daily N, P and K requirements were estimated to be as low as 50, 8 and 60 mg per plant, respectively (Adams 1993).

Nitrogen supply is crucial for tomato yield and quality. Overall, excessive N fertilization may result in low vitamin C contents, delayed maturity and formation of disease-sensitive plant tissues (Weichmann 1991). Parisi *et al.* (2006) reported that a high N application rate impairs some important fruit quality characteristics, such as pH, soluble solids, glucose and fructose content, as well as the ratio of reducing sugars to total solids.

Adequate application of K is a prerequisite for attaining high yield and quality in greenhouse tomato crops. Potassium is highly mobile through the phloem and hence the deficiency symptoms appear in the older leaves; severe K deficiency causes necrosis of the old leaves (**Plate 1A**). A relatively high supply of K enhances several quality attributes of the tomato fruit, including titratable acidity as well as fruit dry matter and total soluble solids content, thereby considerably improving fruit flavour (Fanasca *et al.* 2006a; Passam *et al.* 2007). Furthermore, a high K supply to tomato seems to increase the antioxidant concentration (β-carotene and especially lycopene) during the red and intense-red ripening stages (Fanasca *et al*. 2006b). According to Adams (1999), a shortage of K may considerably degrade the flavour of the tomato fruit, which may become even tasteless. A low rate of K results in fruit ripening disorders (Adams 2002) while an optimum rate improves fruit colour (Passam *et al*. 2007). Moreover, an adequate supply of K improves fruit firmness and consequently its shelf-life (Schnitzler and Gruda 2002). Nevertheless, excess K should be avoided, since it may increase the incidence of blossom-end rot (BER) and other physiological disorders related to low Ca translocation to the fruit.

Optimum P fertilizer is crucial for maximum fruit set and hence high yield in tomato. According to Poulton *et al.* (2001), a high rate of P application to soil-grown tomato increased both the quantity and the quality of pollen, thereby enhancing fitness of the male function. Availability of P to plants is affected by soil temperature with its uptake drastically reduced at soil temperatures lower than 14°C (Lingle and Davis 1959). As a result, P deficiency, which is characterised by the development of purple to violet colour on the undersides of the leaves, may occur even in soils with adequate P levels if the soil temperature drops below 14°C for some time. Generally, symptoms of P deficiency in tomato are associated with P concentrations below 1.3 mg $g^{-1}$ dry weight in the laminae of mature tomato leaves (Besford

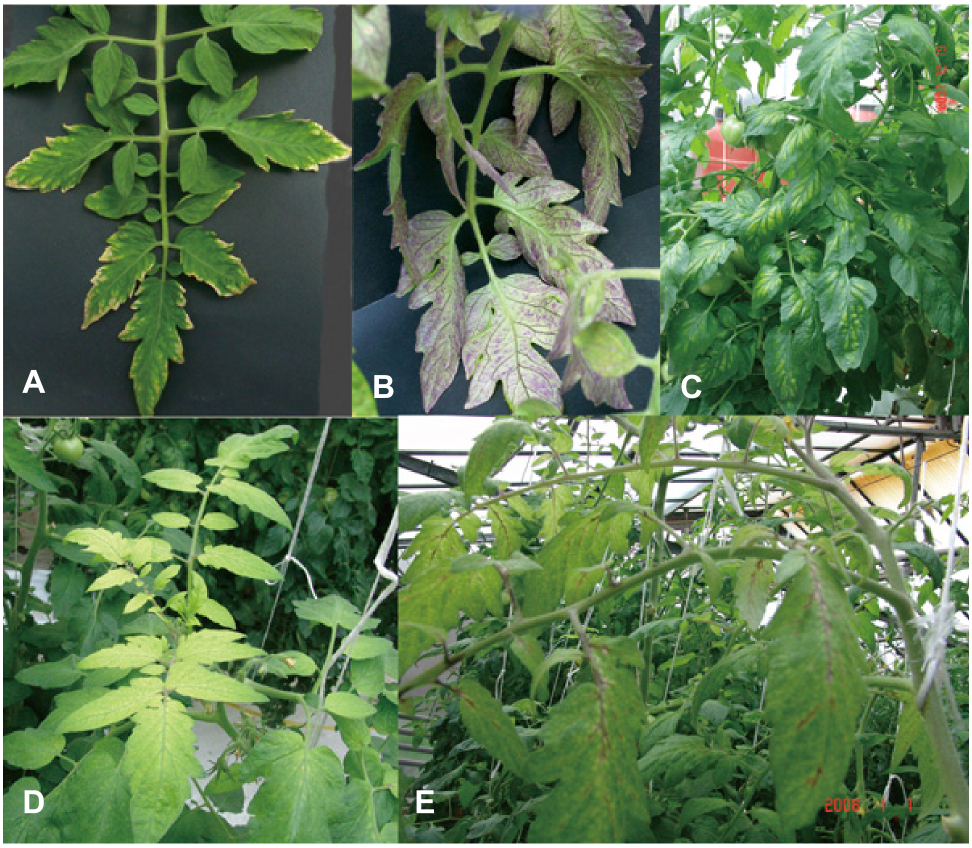


**Plate 1 Symptoms of various nutrient deficiencies in tomato (cv. 'Belladona' $F_1$).** (**A**) K deficiency; (**B**) P deficiency; (**C**) Mg deficiency in plants exposed to excessively high K and Ca; (**D**) Fe deficiency induced by excess Mn; (**E**) Severe Mn deficiency.

*et al.* 1979). With respect to fruit quality, variations in P supply to tomato do not seem to significantly influence the total soluble solids, pH and acidity of tomato juice, or the fruit colour characteristics (Oke *et al.* 2005).

In well managed, fertile greenhouse soils with pH levels ranging from 6 to 7, the Ca, Mg, S and micronutrient requirements of tomato may be covered by the soil reserves. However, the soil fertility has to be checked at least once per year by means of a complete soil analysis and corrected accordingly, if indicated by the results of such an analysis. A high supply of Mg may be beneficial to tomato in terms of fruit quality, by increasing the content of fruit in antioxidative substances such as lycopene and α-tocopherol (Fanasca *et al.* 2006a). In general, a low Ca level in the root zone is rarely a limiting factor for the vegetative growth of tomato (del Amor and Marcelis 2006). However, this nutrient may be crucial at the reproductive stage of the crop due to its involvement in the occurrence of BER (Ho *et al.* 1993; Grattan and Grieve 1999), a physiological disorder of Solanaceous crops. Furthermore, an increased supply of calcium may enhance the resistance of tomato to some pathogens (Yamazaki *et al.* 2000). On the other hand, the level of Ca in the fruit tissue was negatively correlated with tomato lycopene content (Fanasca *et al.* 2006b).

Micronutrient (Fe, Mn, Zn, and Cu) deficiencies are observed at very high pH levels in the soil; hence, the most appropriate way to cope with this problem in the long-term is to properly adjust the soil pH. Iron deficiency in tomato is characterised by a drastic reduction of the leaf chlorophyll content (Dasgan *et al.* 2003). According to Mills and Jones (1996), an Fe concentration of 60 mg $kg^{-1}$ in the leaf petioles opposite or below the top flower cluster is the lowest critical level for the occurrence of Fe deficiency in tomato. The application of chelated micronutrients, especially iron chelate, either via irrigation or by foliar spray is an effective means of preventing or even curing micronutrient deficiencies in soils with unfavourable pH levels (Fernández and Ebert 2005; He *et al.* 2005). Nevertheless, tomato seems to be more susceptible to low than to high pH in the rhizosphere (Islam *et al.* 1980; Akl *et al.* 2003) and this response seems to be at least partly due to the occurrence of Cu toxicity (Chaignon *et al.* 2002). Boron deficiency in greenhouse tomato may occur when the soil B concentration is lower than 1.5 mg $g^{-1}$ of dried soil. At too low B levels in the root zone, the leaves of tomato become brittle and pale-green, a considerable fraction of the flowers abscises and the fruit lack firmness, a problem that is worsened during storage (Smit and Combrink 2004). Furthermore, a sub-optimal B supply may considerably reduce fruit set, especially if no other means for pollination (e.g. vibration) is applied (Smit and Combrink 2005).

## Pepper

Based on some unpublished data from an experiment with pepper (Savvas *et al.* 2007), it was calculated that the mean N, P, K, Ca and Mg requirements of pepper at the reproductive growth stage amount to 180, 30, 220, 80, and 23 mg $plant^{-1}$ $day^{-1}$, respectively. These values were obtained under Mediterranean climatic conditions in a greenhouse crop cultivated from July to November. According to these figures, the total N, P, K, Ca, and Mg requirements of a pepper crop with a plant density of 2.5 plants $m^{-2}$ and a cropping period of 10 months amount to 1350, 220, 1650, 600 and 180 kg $ha^{-1}$, respectively. The above values may be overestimated by 10-15% because at the early growth stage (1-2 months) the daily plant requirements are lower; furthermore, the above values are based on data from a soilless cultivation. In soil-grown pepper crops the nutrient requirements are expected to be lower. The above estimation of the total N requirement of pepper is in agreement with Sonneveld (2002) who reported that the uptake of N by a long-term pepper crop yielding a fresh fruit mass of 25 kg $m^{-2}$ reached 1052 kg $ha^{-1}$. According to Fritz and Stolz (1989), the nutrient uptake of a soil-grown pepper crop yielding 100 tons of fruit reaches 600 kg N, 150 kg $P_2O_5$, 800 kg $K_2O$, and 50 kg MgO. Based on a literature survey, Bosland and Votava (2000) referred to N application rates of 100-300 kg $ha^{-1}$, but this range obviously addresses field-grown pepper crops with a short harvesting period.

The availability of micronutrients, such as Fe, Mn, Zn, and Cu, in soil-grown pepper crops is an issue mainly in calcareous soils characterized by excessively high pH levels. Therefore, if the pH of the soil in pepper crops is not within the optimal range, it is suggested that the leaf micronutrient concentrations should be checked by chemical analysis. Thus, if the concentrations of any micronutrients are not optimal, a foliar micronutrient application may be beneficial, even if no visual deficiency symptoms are observed, because even a latent deficiency may reduce yield. As reported by Anchondo *et al*. (2002), an increase in the Fe supply to an experimental pepper crop significantly enhanced both the relative growth rate and the fruit yield even at a growth stage at which no chlorosis symptoms had appeared. Boron nutrition may also be a problem in calcareous soils, at least if the concentration of hot-water extractable B in the soil is <0.28 mg $kg^{-1}$ (Nabi *et al.* 2006). Nevertheless, the sufficiency range for B is rather narrow and requires careful monitoring. From the results of Nabi *et al.* (2006), a B supply level of 1 mg $kg^{-1}$ of rooted soil, which corresponds to about 3-6 kg $ha^{-1}$, seems to be optimal for pepper.

## Eggplant

Eggplant is a rapidly growing plant with large leaves and, therefore, it is characterized by a high nutrient demand. Recalculation of some data from a previous study (Savvas 1992) with eggplants cultivated in quartz sand for about 6 months at a plant density of 1.5 plants $m^{-2}$ revealed high total removal of N, P, K, and Mg (950, 120, 1380, and 75 kg $ha^{-1}$, respectively). These data are indicative of the magnitude of eggplant nutrient requirements, although it should be taken into consideration that the actual nutrient requirements may vary, depending on growth conditions, genotype, and the length of the cropping period.

In a greenhouse experiment with eggplants grown from mid March to September in Germany (Savvas and Lenz 1995), the daily nutrient uptake per plant was estimated to range from 17-32 mmol N, 1-2.6 mmol P, 9-15.5 mmol K, 3.3-5.3 mmol Ca and 0.9-2.3 mmol Mg from May 27 to September 1. According to the above data, the N and K requirements of eggplant correspond approximately to a N:K ratio of 2 (molar basis). However, the growing period under investigation did not include the early vegetative growth phase, which is characterized by smaller plants and a higher ratio of vegetative to fruit dry mass. This has an influence on the N:K uptake ratio because the leaves are characterized by a higher N:K ratio than the fruit (**Table 1**). This is clearly shown in **Table 1**, which includes concentrations of K and N in leaves and fruit of eggplant and the resultant N:K ratios in each of these plant parts. At the early vegetative growth stage, leaf mass dominates over that of the fruit and hence a higher N:K uptake ratio is anticipated in comparison with that calculated on the basis of the above data. During the reproductive stage of eggplant, the fruits dominate over the vegetative plant parts because fruits constitute stronger sinks for assimilates than the vegetative organs (Lenz 1970), and thus the N:K uptake ratio is reduced.

A study with three rates of N in the form of $KNO_3$ ($N_1$: 15g $m^{-2}$, $N_2$: 22.5g m,$^{-2}$ and $N_3$: 30g $m^{-2}$) reported that an increase in the N rate increased assimilation of $NO_3^-$ to organically-bound N, as well as total and commercial yield of eggplant (López-Cantarero 1998). Furthermore, the crop responded positively to an increase in P rate from 24 to 36 g $m^{-2}$ (López-Cantarero 1998). At the higher P level the plants were able to assimilate more inorganic P to organic P forms, and this was associated with an increase in both total and commercial yield.

**Table 1** Concentrations (mmol $g^{-1}$ dry weight) of N and K in leaves and fruit of eggplants and the resultant N:K ratios in each of these plant parts. Leaves include both lamina and petiole; N includes both nitrate and organically-bound nitrogen.

| Plant part | N | K | N:K |
|---|---|---|---|
| Leaf | 4.12 | 1.91 | 2.16 |
| Fruit | 1.64 | 0.94 | 1.74 |

Data from **Savvas D, Lenz F** (1996) Influence of NaCl salinity on the mineral composition of eggplants in sand culture. *Angewandte Botanik* **70**, 124-127, with kind permission from the Vereinigung für Angewandte Botanik, ©1996.

## NUTRITION IN SOILLESS CULTIVATION SYSTEMS

### Introduction

Soilless culture is becoming increasingly important in greenhouse crops of tomato, pepper and eggplant especially after the phase-out of methyl bromide as a soil fumigant (Batchelor 2004). Soilless culture is capable of improving yield, while providing more efficient tools for managing produce quality due to better control of the conditions prevailing in the root environment (Schnitzler and Gruda 2002; van Os *et al*. 2002).

A major advantage of hydroponics is the precise control of nutrition. This is particularly true for crops grown either on inert substrates or in pure nutrient solution. However, even in soilless crops grown in chemically active growth media, plant nutrition can be better controlled than in crops cultivated in the soil, due to the limited volume of substrate per plant and its standard, homogeneous composition. On the other hand, the limited volume of the root zone in soilless culture demands the optimisation of plant nutrition and irrigation, and relies much more on scientific knowledge and skilful cultural operations than in soil-grown crops. Specialized nutrient solution compositions for soilless-grown tomato, pepper and eggplant crops have been published by Sonneveld and Straver (1994), de Kreij *et al.* (1999a, 1999b) and others. Extensive reviews on the composition and management of nutrient solutions in soilless culture have been published by Savvas (2001), Adams (2002) and Sonneveld (2002).

### Nitrogen nutrition

As a rule, the use of $NH_4$ as sole or dominating N source impairs growth and restricts yield due to the high toxicity of ammonia at an intracellular level (Givan 1979). On the other hand, inclusion of some $NH_4$-N in the nutrient solution supply increases the total cation to anion uptake ratio, thereby stimulating $H^+$ extrusion from the plant cells to the external solution (Imas *et al.* 1997). As a result, the pH in the root environment of the plants is maintained at sufficiently low levels (5.5-6.5). To find a compromise between the above contrasting requirements, a fraction ranging from 5-25% of the total-N supply should be supplied in form of $NH_4$-N (Sonneveld 2002).

### *Tomato*

A total N concentration of about 220 mg $L^{-1}$ is recommended for soilless cultivated tomato crops (Adams 2002). However, this general recommendation needs to be properly adjusted during the cropping period, depending on the stage of plant development (de Kreij *et al.* 1999b). Furthermore, in soilless culture it is important to properly adjust the N:K ratio in the nutrient solution. As reported by Adams and Massey (1984), the mean daily N:K uptake ratios (w/w) observed prior to setting of fruit in the first truss of tomato were 0.86 and 0.81 in February and August, respectively (2.40 and 2.25 on a molar basis). However, when the fruit load on the plants began to increase rapidly, the N:K ratio at which these nutrients disappeared from the solution dropped to 0.4 (1.12 on a molar basis), followed by a slight increase to 0.5 (1.40 on a molar basis) after a few weeks. Comparable results have been found by Voogt and Sonneveld, as cited by van Goor *et al*. (1988).

Many studies have addressed the effects of N source on tomato and its interactions with other nutritional and environmental factors. All these studies have clearly shown that the use of ammonium as sole or dominating N source is detrimental in terms of growth and yield in solution culture, or in chemically inactive substrates (Magalhães and Wilcox 1984; Imas *et al.* 1997; Claussen 2002). The supply of

**Table 2** Effects of the $NH_4$-N/total-N[1] fraction (Nr) in the nutrient solution supplied to tomato grown in a closed hydroponic system on the leaf concentrations of some macronutrients. In each column, values followed by the same letter do not differ significantly at p = 0.05.

| $NH_4$ treatment | P | K | Ca | Mg |
|---|---|---|---|---|
| *Nr* = 0.05 | 7.80 a | 29.0 a | 14.9 a | 4.55 a |
| *Nr* = 0.10 | 7.81 a | 29.9 a | 12.6 b | 4.35 a |
| *Nr* = 0.15 | 7.82 a | 28.9 a | 11.5 c | 4.26 a |
| *Nr* = 0.20 | 8.53 a | 29.2 a | 9.4 d | 3.66 b |
| *Nr* = 0.25 | 7.58 a | 26.9 b | 8.1 e | 3.53 b |

[1]: Total-N = 16.2 mM

Data from **Akl IA, Savvas D, Papadantonakis N, Lydakis-Simantiris N, Kefalas P** (2003) Influence of ammonium to total nitrogen supply ratio on growth, yield and fruit quality of tomato grown in a closed hydroponic system. *European Journal of Horticultural Science* **68**, 204-211, with kind permission from the European Journal of Horticultural Science, ©2003.

**Table 3** Effects of NH4-N/total-N[1] supply fraction (Nr) on growth, yield, fruit quality and incidence of blossom-end rot (BER) in a tomato crop grown in perlite. In each column, values followed by the same letter do not differ significantly at p = 0.05.

| $NH_4$ treatment | Shoot fresh weight (g/plant) | Fruit fresh weight (kg/plant) | Class I fruits (%) | Fruits with BER (%) |
|---|---|---|---|---|
| *Nr* = 0.05 | 3160 a | 11.13 ab | 53.10 c | 0.0 c |
| *Nr* = 0.10 | 3239 a | 12.25 a | 52.70 c | 0.0 c |
| *Nr* = 0.15 | 2741 b | 10.03 bc | 41.30 b | 4.8 c |
| *Nr* = 0.20 | 2586 c | 7.87 d | 15.60 a | 36.9 b |
| *Nr* = 0.25 | 2229 d | 8.60 cd | 13.10 a | 46.1 a |

[1]: Total-N = 16.2 mM

Data from **Akl IA, Savvas D, Papadantonakis N, Lydakis-Simantiris N, Kefalas P** (2003) Influence of ammonium to total nitrogen supply ratio on growth, yield and fruit quality of tomato grown in a closed hydroponic system. *European Journal of Horticultural Science* **68**, 204-211, with kind permission from the European Journal of Horticultural Science, ©2003.

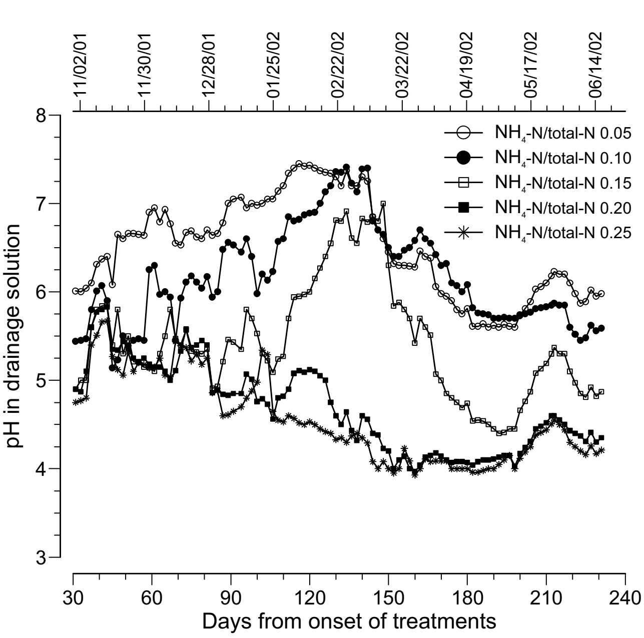


**Fig. 1** Root zone pH in a tomato crop grown in a perlite-based soilless culture system in relation to the ratio of $NH_4$-N/total-N (molar basis) in the supplied nutrient solution. Reproduced from **Akl IA, Savvas D, Papadantonakis N, Lydakis-Simantiris N, Kefalas P** (2003) Influence of ammonium to total nitrogen supply ratio on growth, yield and fruit quality of tomato grown in a closed hydroponic system. *European Journal of Horticultural Science* **68**, 204-211, with kind permission from the European Journal of Horticultural Science, ©2003.

>10% of total-N in the form of ammonium in hydroponically-grown tomatoes may lower the pH in the root zone to less than 5 (**Fig. 1**), with detrimental effects on plant growth and yield. Furthermore, an increase of the $NH_4$-N supply to tomato may increase the severity of BER and other Ca-related disorders in fruit (Pill and Lambeth 1980; Adams 2002; Akl *et al.* 2002). On the other hand, both the growth and the yield of tomato are enhanced when a small part of N is supplied in form of $NH_4^+$ (Sonneveld 2002; Ben-Oliel *et al.* 2004).

As shown in **Table 2**, increasing the $NH_4$-N/total-N ratio ($N_r$) from 0.05 to 0.25 in the nutrient solution supplied to tomato resulted in a progressive restriction of the leaf Ca concentration from 14.9 to 8.1 mg $g^{-1}$ dry weight, whereas the leaf Mg and K levels were reduced only when *N* rose to 0.20 and 0.25, respectively. In contrast, the concentrations of P (**Table 2**) and micronutrients (Akl *et al.* 2003) in the leaves were not affected by varying $N_r$ from 0.05 to 0.25. The impact of $N_r$ in the range 0.05-0.25, on the root-zone pH, vegetative growth, fruit yield, and the incidence of BER in tomato are shown in **Table 3**. Akl *et al.* (2002) reported that tomato is tolerant to moderately high pH but susceptible to low pH levels in the root environment, due mainly to the impairment of Ca uptake. Similar responses of tomato to the rhizosphere pH were found by Islam *et al.* (1980) in a water culture experiment. Since $NH_4$-N has a strong impact on pH, the ammonium to total-N fraction should be adjusted properly in the nutrient solution supplied to tomatoes to avoid a drop of the rhizosphere pH to undesired levels. The results shown in **Fig. 1** as well as those of **Table 2** and **Table 3** clearly show that under Mediterranean mild winter conditions, the $NH_4$-N/total-N ratio in soilless cultivated tomato should normally range between 0.05 and 0.15.

According to Tan *et al.* (2000b), urea can be used as an N-source in soilless grown tomato crops, provided the plants are at the stage of reproductive growth. This recommendation is based on experimental work involving the supply of $^{15}N$-labelled compounds to hydroponically-grown tomato plants. The results revealed poor urea absorption, translocation, and assimilation at the seedling stage, which was followed by increases to almost similar levels with those of $NO_3$-N at the reproductive growth stage.

### *Pepper*

Nitrogen stimulates the vegetative growth of pepper, thereby ensuring high rates of flower formation, fruit set, and assimilate inflow into developing fruits. Indeed, as reported by Schon *et al.* (1994), an increase of the N level in the rhizosphere of pepper grown in rockwool raises the total yield curvilinearly to a maximum threshold. In addition to the total yield, an increase of N up to an optimum level may also enhance some nutritional attributes of pepper, such as the concentrations of lycopene and β-carotene and the antioxidant activity of the lipophilic fraction, as well as its overall commercial quality (Flores *et al.* 2004). Furthermore, the enhancement of the N supply rate may stimulate the uptake of K and P through a synergistic effect of N on both nutrients (Qawasmi *et al.* 1999). Nevertheless, an overdosing of N can stimulate excessive vegetative growth, resulting in large plants with few early fruits and delayed fruit maturity (Bosland and Votava 2000).

Bar-Tal *et al.* (2001a) found that the optimum N concentration for total fruit yield and high fruit quality in soilless-grown pepper crops was in the range of 8.3-9.3 mM. However, according to standard Dutch recommendations for commercial crops grown under North European conditions, the N concentration in the nutrient solution supplied to pepper should be higher, specifically 15.5 mM (Sonneveld and Straver 1994; de Kreij *et al.* 1999a). This high level of nitrogen supply aims firstly at ensuring a constantly high N level in the root zone and secondly to electrochemically compensate for adequate cation supply.

The preferred N source for sweet pepper is usually $NO_3$-N. However, partially replacing $NO_3$-N by $NH_4$-N can increase plant growth and fruit yield, especially under low light intensity or low temperature conditions (Zornoza *et al.* 1988; Marti and Mills 1991; Jung *et al.* 1994; Xu *et al.* 2001). Xu *et al.* (2002) state that 0.9-1.8 mM $NH_4$-N in the nutrient solution increases both the total fruit yield and the efficiency of K-fertilizer use in sweet pepper crops. Bar-Tal *et al.* (2001b) found that an increase in the $NH_4$-N/$NO_3$–N ratio seems to stimulate N uptake. According to these authors, the optimum $NO_3$-N/$NH_4$-N molar ratio for maximal stem dry matter production was 3.5. On the other hand, total and high-quality fruit yields both decreased sharply as the $NH_4$-N concentration in the solution increased to levels above 2 mM (Bar-Tal *et al.* 2001b). Furthermore, increasing the ammonium concentration in the root medium to levels >1 mM decreased the uptake of K and Ca (Marti and Mills 1991; Bar-Tal *et al.* 2001b; Xu *et al.* 2002). The reduction of Ca uptake by the plant may increase the percentage of pepper fruits suffering from BER (Bar-Tal *et al.* 2001a). Therefore, the $NH_4$-N concentration in the nutrient solution supplied to hydroponically-grown peppers should range from 0.5 to 1.5 mM. The exact level should be properly adjusted during the cropping period, depending on the pH measured in the root zone or in the drainage solution.

### *Eggplant*

In a greenhouse experiment with eggplants grown from mid March to September in Germany (Savvas and Lenz 1995), the uptake concentration of N ranged from 5-9.5, with an average value of 8 mmol $L^{-1}$ (**Fig. 2**). These values indicate the target N concentrations in nutrient solutions applied in closed hydroponic systems to compensate for nutrient uptake. However, in open hydroponic systems, the N concentration in the nutrient solution supplied to eggplants should normally be higher so as to buffer temporal N fluctuations in the root zone and allow for an adequate supply of macronutrient cations. According to Voogt (1986), a total-N concentration of 16 mM is recommended for eggplants grown in rockwool. This concentration may be applied to eggplant crops grown not only in rockwool, but in other inert substrates as well.

With respect to the N source, nitrate should be the dominating form, but it is advisable for a small part of the total supply to be applied in the form of $NH_4$-N (Elia *et al.* 1996) since this provides efficient control of pH in the root zone at levels below 7, which are favourable for P and micronutrient uptake. On the other hand, overdosing with $NH_4$-N may result in too low pH in the root zone, which may be harmful for plant growth, yield and fruit quality (Savvas, unpublished data). Currently, the available information in the international literature on the responses of eggplant to the N sources, and specifically to the $NH_4$-N/total-N ratio, is limited. According to de Kreij *et al.* (1999b), a $NH_4$-N concentration of 1.5 mM in the nutrient solution, which corresponds to a $NH_4$-N/total-N ratio of 0.09, is recommended for eggplants grown in soilless culture systems.

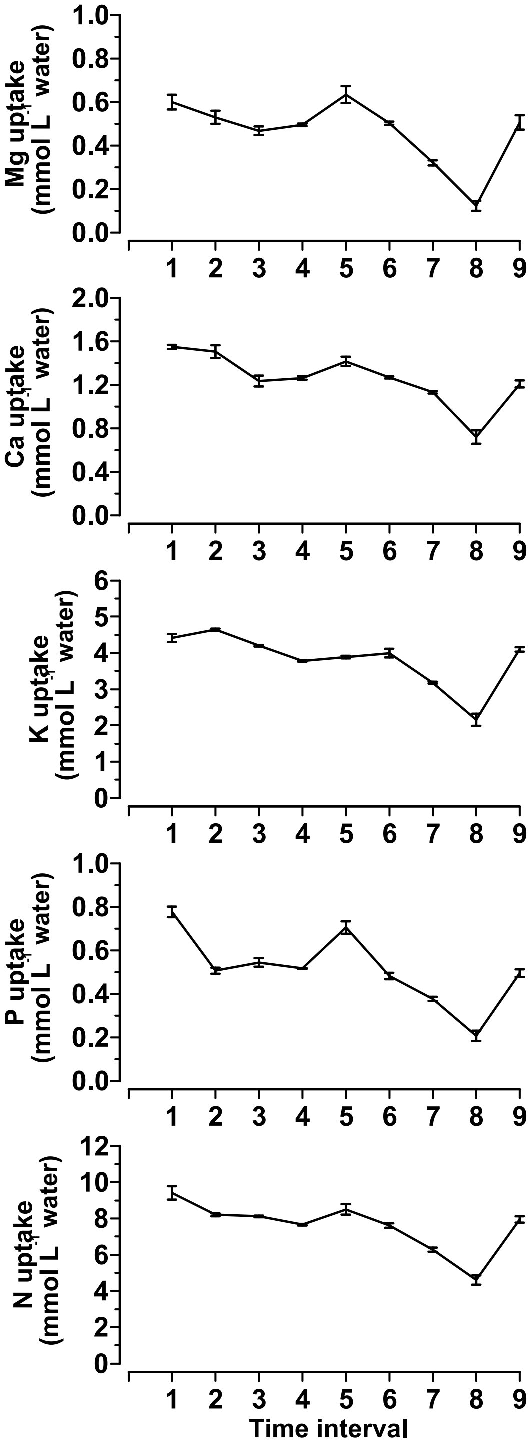


**Fig. 2** Nutrient to water uptake ratio of some macronutrients for eggplant grown in a recirculating nutrient solution. Values were calculated as means of nine successive fortnight intervals in the time from 27/05 to 29/09. Vertical bars indicate standard errors of means ($n$ = 4). Reproduced from **Savvas D, Lenz F** (1995) Nährstoffaufnahme von Aubergine (*Solanum melongena* L.) in Hydrokultur. *Gartenbauwissenschaft* **60**, 29-33, with kind permission from the Vereinigung für Angewandte Botanik, ©1995.

## Phosphates and sulphates

### *Tomato*

An adequate supply of phosphorus to soilless grown tomato crops is a prerequisite for optimal development and high yields. A shortage of P in soilless culture is first indicated by the retarded expansion of the older leaves, which curl towards the underside, and a reddish coloration of petioles and leaf veins (**Plate 1B**). Nevertheless, an excess of P in the nutrient solution should be avoided, since, in addition to direct toxic effects on the plants, it may result in Ca, Mg and micronutrient precipitation. The proportion of P to the total anions in the hydroponic nutrient solutions should be maintained at relatively low levels (usually <0.1), otherwise precipitation of phosphoric salts may occur (De Rijck and Schrevens 1998b).

Steiner (1966), in an experiment with tomato, explored the $NO_3^-$:$SO_4^{2-}$ ratio and found that $NO_3^-$:$SO_4^{2-}$ ratios as high as 0.86 may result in a small yield decrease compared to lower ratios ranging from 0.67 to 0.36. Nukaya *et al.* (1991), working with a constant nutrient solution EC of 3.5 dS $m^{-1}$ did not find any significant differences in tomato fruit yield when the $NO_3^-$:$SO_4^{2-}$:$Cl^-$ ratio (molar basis) in the recirculating nutrient solution varied between (0.20-0.55) : (0.17-0.34) : (0.10-0.45), respectively, but the treatments with the highest sulphate proportions tended to have slightly higher yields. Overall, tomato seems to be favoured by a relatively high sulphate concentration in the root zone. De Kreij *et al.* (1999b) suggested a concentration of 6.8 mM $SO_4^{2-}$ in the root zone of tomato, whereas Lopez *et al.* (2002) recommend a higher level (10.4 mM) for optimal uptake. Moreover, tomato seems to tolerate even higher sulphate concentrations than 10.4 mM in the root zone (Lopez *et al.* 1996).

## Pepper

Soil-grown peppers were found to respond positively to an increased sulphur supply in form of $(NH_4)_2SO_4$ (Smatanová *et al*. 2004). However, information regarding the responses of pepper to sulphur in soilless culture is scarce. According to Dutch recommendations, a $SO_4^{2-}$ concentration of 1.75 mM should be established in nutrient solutions supplied to hydroponically-grown peppers, aiming at a level of 3 mM in the root environment (Sonneveld and Straver 1994). The corresponding recommendations for phosphates are 1.25 mM in the nutrient solution supplied to the crop and 1.2 mM in the root environment. When the drainage solution was recycled, a $SO_4^{2-}$ concentration of 1.20 mM and a $H_2PO_4^-$ concentration of 1 mM in the fresh nutrient solution introduced to the closed-cycle cultivation system to compensate for nutrient and water uptake proved efficient under Mediterranean climatic conditions (Savvas *et al*. 2007). In addition to the absolute P concentration in the supplied nutrient solution, frequent irrigation may increase the availability of P in the rhizosphere and thereby improve the performance of soilless-grown pepper crops (Silber *et al.* 2005).

## Eggplant

There is hardly any information in the international literature concerning the responses of eggplant to sulphates in soilless culture. De Kreij *et al.* (1999a) recommend a $SO_4^{2-}$ concentration of 1.5 mM for nutrient solutions supplied to soilless-grown eggplants. With respect to phosphorus, eggplant seems to be favoured by concentrations up to 1.75 mM in the supplied nutrient solution (Zipelevish *et al.* 2000). According to these authors, an increase in the average P concentration in the nutrient solution from 36 to 54 mg $L^{-1}$ enhanced the number of fruits per plant as well as that of 1st class fruits, although the total fruit yield was not significantly influenced by the elevation of the P supply. Nevertheless, one should take into consideration that the P uptake concentration does not exceed a level of 0.8 mmol $L^{-1}$ in eggplant crops (**Fig. 2**). Furthermore, high P levels entail an increased risk of precipitation of phosphate salts, particularly at pH values >6.2, as well as a restriction of Fe, Mn, and Zn uptake (Sonneveld 1989, 1995). In view of this, a $H_2PO_4^-$ concentration ranging from 1.20-1.40 mM in the supplied nutrient solution seems more reliable for hydroponically grown eggplants.

# Macrocations

## Tomato

As reported by Adams and Grimmet (1986), high yields of tomatoes can be obtained even with relatively low levels of potassium in the nutrient solution, provided a minimum concentration is constantly maintained in the root zone. Nevertheless, the K requirements of tomato are extraordinarily high due to the rapid growth of the plant in combination with the heavy fruit load (Chapagain and Wiesman 2004). To ensure an adequate K level in the root zone of tomato, a K concentration of 7 mM in the nutrient solution has been suggested for commercial tomato crops (Welleman and Verwer 1983, cited by Hannan 1998), while Sonneveld (2002) recommends a K level of 8 mM in the root zone. Schnitzler and Gruda (2002) and Adams (2002) suggest a K concentration of about 10 mM in the root environment to obtain fruits with good flavour and external quality and to reduce the incidence of ripening disorders. However, according to Bar-Tal *et al.* (1996), K concentrations as high as 10 mM in the root zone of tomato may restrict Ca uptake, thereby appreciably increasing the incidence of BER (see also under 'Physiological disorders of the Solanaceae'). The discrepancy in the above-referenced recommendations seems to reflect different requirements under different environmental conditions. The recommendations of Schnitzler and Gruda (2002) and Adams (2002) are based on experiments conducted in North Europe, while the report of Bar-Tal *et al*. (1996) originates from research conducted in Israel.

The Ca concentrations suggested for nutrient solutions supplied to hydroponically-grown tomatoes range from 4-5.5 mM. At the early vegetative growth stage, even lower Ca concentrations seem to be sufficient for optimal growth (del Amor and Marcelis 2006). An inadequate delivery of Ca to the foliage of tomato is likely to occur only under conditions of rapid growth combined with high air humidity, which restricts the rate of transpiration and thus the rate of Ca transport to the leaves via the xylem (Soneveld and Welles 1988). However, at the reproductive growth stage, the Ca concentration in the root zone requires special attention, since the fruit of tomato is often affected by physiological disorders related to either insufficient or excessive Ca translocation to the fruit tissues. The involvement of Ca in the occurrence of Ca-related physiological disorders in tomato is discussed in more detail in the section 'Physiological disorders of the Solanaceae'. The target level of Ca in the root zone of tomato amounts to 10 mM (Sonneveld 2002).

High levels of Mg in the root zone seem to be beneficial for tomato (Sonneveld 1987). According to Adams (2002), a Mg concentration of approximately 2 mM in the root zone of tomatoes grown in NFT resulted in deficiency symptoms in the leaves, while increasing the Mg level to 3 mM kept the plants healthy throughout the season. Similar results were reported by Hao and Papadopoulos (2003, 2004) for tomato grown on rockwool. Sonneveld (2002) suggests an optimum Mg concentration of 4.5 mM in the root zone of tomato grown in rockwool. According to Schnitzler and Gruda (2002), magnesium deficiency (**Plate 1C**) is more likely to occur under conditions of low humidity and a high supply of Ca, K and $NH_4$.

A preliminary evaluation of some unpublished data (Savvas and Ntatsi, unpublished) has indicated that the K, Ca, and Mg concentrations in the nutrient solution supplied to tomato grown in open hydroponic systems under Mediterranean growing conditions should range from 6.5-7.75, 4.25-5.0 and 2.0-2.75 mM, respectively, depending on the stage of plant development.

## Pepper

Sonneveld and Voogt (1985a) stated that pepper is not very sensitive to variations of the K: Ca: Mg ratio in the nutrient solution contained in the root environment. However, in most cases, the level of Ca in the root zone of hydroponically-grown pepper should be maintained at relatively high levels, specifically close to 8 mM (Sonneveld 2002) due to the high susceptibility of this plant species to BER (Bosland and Votava 2000). To maintain this Ca level in the root zone, Ca concentrations ranging from 4-5 mM in the nutrient solution supplied to the plants are recommended. Furthermore, to prevent shortages of both Mg and Ca in the leaves and fruits of soilless grown pepper, the K level in the root zone should be not higher than 6 mM (Sonneveld 2002), which can be attained by providing 6.5-7.0 mM K in the nutrient solution supplied to the plants (de Kreij *et al*. 1999a). The corresponding levels recommended for Mg in soilless-grown pepper crops are 3 mM in the root zone (Sonneveld 2002) and 1.5 mM in the nutrient solution supplied to the crop.

## Eggplant

According to Sonneveld and Voogt (1985a), eggplant is favoured by an increased supply of Mg. Typically, Mg concentrations as high as 2.5 mM are suggested for the nutrient solution supplied to eggplant, while the target Mg concentration in the root zone is 4.5 mM (de Kreij *et al.* 1999a). In comparison to tomato and pepper, eggplant has a lower Ca requirement, as indicated by the low apparent Ca uptake concentration found by Savvas and Lenz (1995), which was invariably less than 1.6 mmol $L^{-1}$ of water (**Fig. 2**).

Savvas and Lenz (1995) found that the daily uptake per plant ranged from 9-15.5 mmol K, 3.3-5.3 mmol Ca and 0.9-2.3 mmol Mg for eggplant grown in recirculating nutrient solution from May 27 to September 1. The corresponding nutrient to water uptake ratios were 2.5-5 mmol $L^{-1}$ K, 0.9-1.6 mmol $L^{-1}$ Ca and 0.15-0.7 mmol $L^{-1}$ Mg (**Fig. 2**), while the average values were 4.1, 1.4 and 0.5 mmol $L^{-1}$, respectively. These data are especially important for the compilation of nutrient solution recommendations for closed hydroponic systems. However, they can be used to establish nutrient solution recommendations for open hydroponic systems as well. De Kreij *et al*. (1999b) suggests concentrations of 6.75 mM K, 3.25 mM Ca and 2.5 mM Mg in nutrient solutions used in open hydroponic systems, while Voogt (1986) recommends 7.75, 3.75 and 2.0 mM, respectively.

## Micronutrients

### *Tomato*

Adams (2002) suggested Fe concentrations of 8-10 mg $L^{-1}$ for tomato crops grown in NFT in order to avoid foliar symptoms of Fe deficiency throughout the cropping season. However, Sonneveld and Voogt (1985b) and Sonneveld and Straver (1994) recommended a concentration range of only 10-15 μM (0.55-0.84 mg $L^{-1}$) for tomato grown in rockwool, aiming at a concentration of 25 μM in the root environment. According to our experience, the level suggested by Sonneveld and Voogt (1985b), seems to be sufficient under practical growing conditions not only for rockwool, but also for other inert substrates such as perlite and pumice, provided it is supplied in the form of Fe-chelates. Nevertheless, in tomato crops grown in NFT, the Fe concentration in the recirculating nutrient solution should be higher than the levels suggested for rockwool-grown crops (Sonneveld and Voogt 1985b). According to Adams (2002), the lower Fe requirements of tomato grown in rockwool in comparison with NFT may be partly due to some release of Fe from the substrate. However, Sonneveld and Voogt (1985b) suggest that differences in root branching and root hair density between the two soilless cultivation systems may also be involved in the dissimilar responses of tomato to the Fe level in the root zone. Nevertheless, even in NFT, a Fe concentration of 20 μM in the fresh nutrient solution added to the system, which resulted in a mean level of 46 μM in the root zone, proved to be sufficient for tomato (Sonneveld and Voogt 1985b). Much higher Fe levels in the solution supplied to the crop entail the risk of chelate accumulation in the root zone, which may be toxic for plant growth (Wallace *et al*. 1976; Sonneveld and Voogt 1985b). With respect to the type of Fe-chelate, EDTA seems to be the best Fe source in NFT (Adams 2002), whereas there was no difference between the four chelates tested in rockwool (Sonneveld and Voogt 1985b).

The standard recommended concentration of Mn in the Netherlands is 10 μM for tomato grown in rockwool, which corresponds to 0.55 mg $L^{-1}$ (Sonneveld and Straver, 1994; de Kreij *et al*. 1999b). According to Adams (2002), there was little response of tomato to Mn concentrations in the range 0.2-1.25 mg $L^{-1}$ in the root environment, but symptoms similar to those of Fe deficiency were induced when a Mn concentration of 3.13 mg $L^{-1}$ was maintained in the solution. **Plate 1D** shows symptoms of Fe deficiency induced by raising the Mn concentration to 120 μM (6.8 mg $L^{-1}$) in the recirculating nutrient solution (Savvas *et al*. unpublished), while **Plate 1E** shows symptoms of severe Mn toxicity, which were observed when the Mn concentration in the root zone was further raised to 155 μM (8.5 mg $L^{-1}$).

According to Adams (2002), the concentrations of both Cu and Zn in hydroponic nutrient solutions supplied to tomato should range from 0.3-0.4 mg $L^{-1}$, while levels of 0.2 mg $L^{-1}$ or less are too low to maintain healthy plant growth in NFT. Sonneveld and Straver (1994) suggested a similar level for Zn (5 μM, which corresponds to 0.33 mg $L^{-1}$) but an appreciably lower level for Cu (0.75 μM, which corresponds to 0.05 mg $L^{-1}$). Preliminary unpublished data of Savvas and Ntatsi for a tomato crop grown in a closed hydroponic system using perlite as the growth medium indicate that Zn and Cu disappeared from the recycling nutrient solution at average rates of 3.3 and 0.2 μmol $L^{-1}$ of absorbed water. These results indicate that a Cu concentration of 0.5-0.6 μM in the nutrient solution supplied to hydroponically-grown tomato crops is sufficient under Mediterranean growing conditions. This suggestion is also in agreement with our experience from commercial hydroponic tomato crops, which indicates that 0.5-0.75 μM Cu were sufficient for high fruit yield. However, high Cu concentrations in the supplied nutrient solution should be avoided due to the risk of Cu toxicity which, according to Liao *et al.* (2000), is likely to occur at Cu concentrations higher than 5 mg $L^{-1}$ in the nutrient solution.

A low boron concentration of 0.1 mg $L^{-1}$ (nearly 10 μM) had surprisingly little effect on tomato yield, which was reduced by only 13% during the first four weeks of harvest (Adams 2002). Smit and Combrink (2004) observed B deficiency symptoms at a B concentration of 0.02 mg $L^{-1}$ (nearly 2 μM) in the nutrient solution supplied to tomato grown on inert substrates. A boron concentration of 0.16 mg $L^{-1}$ seemed to be optimal for tomato and levels up to 0.64 mg $L^{-1}$ did not cause any toxicity symptoms in the plants. Massey *et al*. (1986) state that B concentrations as high as 1 mg $L^{-1}$ (nearly 90 μM) may cause mild toxicity symptoms while 2 mg $L^{-1}$ is expected to impose clear symptoms of B toxicity in tomato grown in recirculating nutrient solution. Sonneveld and Straver (1994) suggested a B concentration of 30 μM in the nutrient solution supplied to rockwool-grown tomato and 50 μM in the root environment.

With respect to molybdenum, there is virtually no literature concerning the optimal concentration range of this nutrient in soilless culture. Currently, the standard recommendation for Mo in nutrient solutions used in soilless culture is 0.5 μM (de Kreij *et al*. 1999b).

### *Pepper*

The recommended concentrations of micronutrients in nutrient solutions supplied to soilless cultivations of pepper are generally similar to those suggested for tomato (de Kreij *et al*. 1999a). However, the optimum concentrations of Mn and Fe in the root zone of pepper are lower than those recommended for tomato, while that of B is higher. According to Sonneveld and Straver (1994), the optimum Fe, Mn, Zn, Cu, B and Mo concentrations in the root zone of hydroponically-grown pepper are 15, 5, 7, 0.7, 80 and 0.5 μM, respectively.

As reported by Anchondo *et al*. (2002), low Fe levels (1 or 3 μM) in the external nutrient solution were associated with reduced relative growth rates, while an elevation of the Fe concentration to 10 or 30 μM increased fruit yield and total plant dry matter. Increasing Fe to levels ranging from 10-30 μM in the nutrient solution enhanced both ferrous and total iron in the leaves of pepper, but depressed foliar Cu and P, while the leaf Zn, Mn, and K concentrations were not influenced by Fe level between 1-30 μM in the nutrient solution (Anchondo *et al*. 2001). One should not rely on the absence of visible chlorotic symptoms to conclude that the Fe supply to pepper is adequate. Indeed, as reported by Anchondo *et al.* (2002), low Fe concentrations in the supplied nutrient solution may restrict the relative growth rates before the appearance of chlorosis.

The concentrations of Mn in both leaves and fruit may be significantly reduced under saline conditions (Aktas *et al.* 2005). Hence, under salt stress conditions, the Mn concentration in the nutrient solution supplied to hydroponically-grown pepper crops should be somewhat higher than the standard recommended levels.

According to Cornillon and Palloix (1997), high leaf Zn concentrations in pepper were linked to a sharp reduction in growth, although no Zn toxicity symptoms were visible.

This result indicates that the level of Zn in the root zone of hydroponically grown pepper should never be left to increase to higher levels than those considered as standard in commercial practice (6-8 μM).

Recent experimental work has indicated that young pepper seedlings are much more susceptible to excessive Cu concentrations in the root zone than fully grown plants (Zheng *et al*. 2005). At the seedling stage, plant leaf number, leaf area, leaf biomass, specific leaf area, stem length and shoot biomass were suppressed at Cu levels higher than 0.19 mg $L^{-1}$. When plants reached 11 weeks old, Cu started to show significant negative effects on leaf and shoot biomass only when its external concentration increased to 1.05 mg $L^{-1}$ or higher.

### *Eggplant*

One can hardly find any peer-reviewed information in the international literature regarding the micronutrient requirements of soilless-grown eggplants. According to the practical recommendations of Voogt (1986), the concentrations of Fe, Mn, Zn, Cu and Mo in the nutrient solutions supplied to eggplants should amount to 15, 10, 5, 0.75 and 0.5 μM, respectively. With respect to boron, there is a report (de Kreij and Basar 1997) indicating that eggplants are susceptible to B deficiency, which is manifested by yellowing of the distal ends of the young, fully developed leaves if the B concentration in the supplied nutrient solution is within the range of 0-20 μM. Nevertheless, as long as leaf tip yellowing is maintained at moderate levels, the B deficiency is rather mild and has no negative effect on fruit production.

## PHYSIOLOGICAL DISORDERS OF THE SOLANACEAE

Most physiological disorders of the Solanaceae result from a complexity of factors related to environmental conditions, nutrition and irrigation, although in many instances only one of these may be recognized as a major cause. In this section, physiological disorders that are mainly caused by nutritional and irrigation factors and affect fruit quality are presented.

### Tomato

### *Blossom-end rot (BER)*

Blossom-end rot (BER) is a frequently occurring physiological disorder of the tomato fruit, which appears as a leathery brown patch at the blossom-end of the fruit (**Plate 2A**). In BER-susceptible cultivars, this disorder may cause a high proportion of internal BER, which is often not visible from the exterior of the fruit (Adams and Ho 1992). BER occurs mainly during the hot, dry season of the year, under conditions of low air humidity (Bertin *et al.* 2000) and is ascribed to a local shortage of Ca in the distal part of the fruit, which results in tissue disorganization due to impairment of plasma membranes and/or cell walls (Ho 1989; Adams 2002).

Low Ca concentrations in the root zone are in most cases associated with a higher incidence of fruit affected by BER (De Kreij *et al*. 1996; Fanasca *et al*. 2006a), although too high Ca levels may also aggravate the occurrence of this disorder (Savvas and Ntatsi, unpublished data). Nevertheless, an appreciable body of research has indicated that the correlation between the Ca concentration in any part of the tomato fruit and the occurrence of BER is in most cases poor (Dorais and Papadopoulos 2001). To date, a critical fruit Ca concentration associated with the occurrence of BER in tomato has not been established (Taylor and Locascio 2004). The poor correlation between the fruit Ca level and the appearance of BER was used as an argument by some investigators to challenge the notion that BER is a calcium-related disorder (Saure 2001). Other investigators tried to refine the concept based on the assumption that BER is a Ca-related disorder (Taylor and Locascio 2004; Ho and White 2005). According to this approach, the damage in fruit cells occurs during a period of rapid cell elongation which may result in a transient Ca shortage. However, the visible symptoms and the sampling for Ca measurements take place later, when normal Ca supply may have recovered.

Besides the absolute Ca level in the root zone, the concentrations of K and Mg as well as the Ca: K and Ca: Mg ratios have a strong impact on the incidence of BER. Thus, Willumsen *et al.* (1996), found that an increase of the K and Mg activities and a reduction of the Ca activity in the root environment favour the occurrence of BER in tomato fruits. According to Hao and Papadopoulos (2004), the incidence of BER at 150 mg $L^{-1}$ Ca increased linearly with increasing Mg concentration, while at 300 mg $L^{-1}$ Ca it was not affected by Mg concentration. Similarly, Nukaya *et al.* (1995) found that raising the K: Ca ratio in the nutrient solution increases the incidence of BER. In addition to K and Mg, high external $NH_4^+$ levels may also depress the uptake of Ca by tomato, thereby increasing the number of fruits affected by BER (Kirkby and Mengel 1967; Siddiqi *et al*. 2002; Akl *et al.* 2003).

High NaCl-salinity results in a higher proportion of fruits with BER (Sonneveld and Van der Burg 1991). However, a moderate increase in $Cl^-$ without raising the Na levels in the root zone or the total salt concentration seems to decrease the occurrence of BER, probably because $Cl^-$ enhances the uptake of $Ca^{2+}$ (Nukaya *et al*. 1991). Increased salinity in the root zone of tomato due to higher nutrient concentrations than the standard recommended values may also increase the incidence of BER (Sonneveld and Welles 1988; Savvas and Ntatsi, unpublished data). The above results indicate that the occurrence of BER is stimulated by the low osmotic potential prevailing in the root zone rather than by the specific salts being in excess in the root zone. This consideration is in agreement with older findings indicating that a shortage of water in the root zone of tomato considerably increases the number of fruit affected by BER (van Goor 1974).

Blossom-end rot in tomato is strongly influenced by environmental conditions, such as air RH, air and root temperature, and solar radiation intensity (Dorais and Papadopoulos 2001; Peet 2005). As summarized by Adams (2002), low air RH, high air and root temperatures and high solar radiation intensity may considerably increase the incidence of BER. Low air RH (high vapour pressure deficit) seems to be the most important environmental factor in increasing the occurrence of BER (Bertin *et al.* 2000). In cultivars that are not susceptible to BER, a rather low impact of these climatic parameters is anticipated, if the uptake and translocation of Ca within the plant is not additionally impaired by water stress or high K, Mg, or Na levels in the root zone.

### *Gold spots and gold specks*

Gold specks or spots (**Plate 2B**) are observed around the calyx and shoulders of mature fruit (Peet 2005). According to de Kreij *et al*. (1992), this abnormality is caused by an excess of Ca deposition in the cell walls of the fruit. Den Outer and van Veenendaal (1988) observed a granular mass consisting of calcium salt crystals, presumably calcium oxalate, in cells of affected tissues. The occurrence of gold specks depends also on genotypic differences among cultivars (Ilker *et al.* 1977). In general, cultivars resistant to BER are more susceptible to the occurrence of gold spots and *vice versa* (Ho *et al*. 1999).

High air humidity, which enhances the translocation of Ca to the fruits when it is combined with high Ca: K ratios in the root zone, may significantly increase the incidence of gold specks on tomato fruit (de Kreij *et al*. 1992). Conversely, Nukaya *et al*. (1995) observed a decrease in the incidence of gold specks on tomato fruit when the Ca: K ratio in the root environment was reduced. Furthermore, raising $Cl^-$ resulted in an increased incidence of gold specks, which also affected the shelf life of the fruit, probably because $Cl^-$ enhances the uptake of $Ca^{2+}$ (Nukaya *et al*. 1991).


**Plate 2 Fruit disorders caused by nutrient deficiencies.** (**A**) Tomato (cv. 'Belladona' $F_1$) blossom-end rot; (**B**) Tomato (cv. 'Belladona' $F_1$) gold speck; (**C**) Tomato (cv. 'Belladona' $F_1$) radial cracking; (**D**) Pepper (cv. 'Calyx' $F_1$) blossom-end rot; (**E**) Eggplant (cv. 'Leanda' $F_1$) internal fruit rot.

## *Blotchy ripening and grey wall*

There are several fruit colour disorders which affect greenhouse tomato crops, thereby considerably reducing their economic value and even rendering them either non-marketable or Class II (Darrigues *et al.* 2008). The term 'blotchy ripening' is used to indicate poorly ripened fruits, which are characterized by an uneven rate of ripening at different areas of their surface. Thus, while most of their surface has turned red at ripening, some patches remain green, or grey, or have turned yellow. When grey patches are prevalent, the disorder may also be characterized as 'grey wall'. Beneath the epidermis, parts of the fruit flesh show an uneven coloration and some areas may be a brown colour. Some of the blotchy ripening symptoms in tomato fruits are similar to those caused by virus infections, specifically tobacco/tomato mosaic virus (TMV/ToMV). The presence of visible TMV symptoms in the foliage of tomato, such as mottling and distortion, is the only safe visible criterion that can be used to distinguish the viral infection from the physiological disorder.

Blotchy ripening is more likely to occur at relatively low nutrient concentrations in the root zone (Sonneveld and Welles 1988). Some authors reported an association between grey wall and low K supply (Picha and Hall 1981). Furthermore, Dangler and Locascio (1990) found that an increase in N application reduced the incidence of internal blotchy ripening. Adams *et al.* (1987) found negative relationships between the percentage of unevenly ripened fruits and the K and N levels in the root zone of tomato grown in peat. However, Bar-Tal (1994) found no significant effect of $NO_3$ concentration in the nutrient solution on blotchy ripening.

Blotchy ripening is more prevalent when temperatures are very high and the solar radiation intensity is rather low (Rylski *et al*. 1994). Furthermore, the incidence of blotchy ripening seems to be positively related to fruit size (Rylski and Avraham 1980, cited by Bar-Tal *et al.* 1994). In agreement with this consideration, root pruning in tomato restricted the occurrence of blotchy ripening and fruit size to the same degree (Bar-Tal *et al*. 1994).

## *Yellow shoulder*

Yellow shoulder (YSD) is a ripening disorder characterized by discoloration of the proximal-end tissues of the fruit, which remain yellow or green, while the remainder of the fruit surface turns red. According to Francis *et al.* (2000), a typical feature of YSD is the presence of discoloured regions beneath the epidermis of ripening tomato. Both colour and colour uniformity are affected by YSD. According to Picha (1987) and Darrigues *et al.* (2008), YSD significantly reduces the level of lycopene in affected tissue as well as in the juice extracted from affected fruit. The levels of β-carotene are also reduced in affected tissue, but not in juice originating from this tissue (Darrigues *et al.* (2008). As reported by Sacks and Francis (2001) and Hartz *et al.* (2005), there are significant genotypic differences among cultivars with respect to their susceptibility to YSD.

Environmental factors such as high RH (Picha 1987), large temperature fluctuations (Jones and Alexander 1962) and high pericarp temperatures (Picha 1987) contribute to a higher frequency of fruits with YSD. Moreover, the incidence of YSD seems to be influenced by the K, N and P supply (Clivati-McIntyre *et al*. 2007). For example, a shortage of K during early fruit set may increase the percentage of fruits suffering from YSD (Hartz *et al*. 1999, 2005), but subsequent foliar applications of K do not mitigate the occurrence of the disorder (Hartz *et al*. 2005). As stated by Hartz *et al.* (2005), enhanced fertilization with potassium improves fruit colour, while at the same time reducing the incidence of yellow shoulder and other fruit colour disorders.

## *Fruit cracking*

Cracking is a disorder that occurs when the internal fruit expansion is faster than that of the epidermis, thereby resulting in splitting of the latter. The fruit become more susceptible to this disorder as they mature, especially as colour develops. Fruit cracking in tomatoes is caused by a combination of several factors, mainly associated with the water balance of the fruit (Peet 1992). It seems that rapid changes in the water potential of the fruit may result in tissue cracking. However, the resistance of cell walls and membranes to the driving force for cracking also plays a crucial role in the occurrence of this disorder. Hence, factors contributing to the reinforcement of these structures may reduce the incidence of fruit cracking (Emmons and Scott 1998). Calcium is one of these factors and at least some types of cracking might be considered Ca-related disorders. In general, adequate transport of Ca to the tomato fruit was found to reduce both the number of cracked fruit and the severity of cracking (Licter *et al*. 2002). According to Bangerth (1973), immersion of tomato fruits in a Ca solution inhibits cracking. In agreement with this, Lichter *et al*. (2002) found that the addition of Ca to the water reduces fruit cracking whereas chelating agents increase the occurrence of this disorder.

Basically, three different types of tomato cracking may be distinguished: radial, concentric and cuticular. Radial cracking starts from the stem scar and progresses toward the blossom end (**Plate 2C**), while concentric cracking develops in circles as a ring or a series of rings around the stem scar (Grierson and Kadar 1986). These two types of cracking are more frequent and sometimes they appear simultaneously on the same fruit. Therefore, they are generally considered to be the most important types of cracking (Cortes *et al*. 1983), although in some countries cuticle cracking may cause more severe economic damage (Bakker 1988). Cortes *et al.* (1983) stated that radial and concentric cracks are controlled by partially different genetic systems. Cuticular cracking is also widely known as 'russeting' (Bakker 1988; Ehret *et al*. 2008).

In recent years, an additional type of cracking termed 'shoulder check' cracking has been recognized (Lichter *et al*. 2002; Huang and Snapp 2004a).This disorder appears as a surface roughness that develops primarily on the shoulder of the fruit, which spoils the appearance and resricts the storability of the fruit (Huang and Snapp 2004a).

Radial cracking seems to be associated mainly with the water status in the root zone. Thus, according to Peet and Willits (1995) and Peet (2005), excessive irrigation and high levels of soil moisture increase the occurrence of radial cracking in tomato crops grown both in greenhouse and in the field. The irrigation frequency is also a factor. Overall, irrigation frequency that results in large fluctuations in the soil moisture status is associated with a high incidence of radial cracking. A higher irrigation frequency with smaller amounts of water per irrigation event may reduce the occurrence of radial cracking. For example, Abbott *et al.* (1986) reported that fruit cracking can be reduced by increasing the irrigation frequency from 1 to 4 times a day.

Cuticle cracking, or russeting, is one of the most serious problems affecting the external quality of greenhouse-grown tomatoes (Ehret *et al.* 2008). The damage caused by this disorder is due to the occurrence of very fine hair-like cracks that, unlike radial or concentric cracks, are largely confined to the cuticle of the affected fruit. The cracks are randomly oriented and form a network all over the fruit surface (Bakker 1988). Cuticle cracking seems to occur when the expansion of the epidermis cannot keep peace with fruit enlargement (Kamimura *et al*. 1972, cited by Bakker 1988). Several studies have demonstrated the importance of the greenhouse environment in the development of cuticle cracking. According to Dorais *et al*. (2004), cuticle cracking is positively and linearly correlated with the average day/night temperature differential, but with respect to air humidity, contradictory reports occur. Bertin *et al*. (2000) and Leonardi *et al*. (2000) found that a low VPD (high RH) increases cuticle cracking. More recently, however, Demers *et al*. (2007) did not find any causal relationship between the occurrence of russeting in tomato fruits and the day/night RH. Light has been shown to be positively correlated with the occurrence of cuticle cracking in tomato (Ehret *et al.* 1993), and greenhouse shading reduces the incidence of this disorder (Dorais *et al*. 2004). Emmons and Scott (1997) suggested that fruit exposed to direct sunlight had a significantly greater incidence of russeting than fruit that were shaded by the plant foliage. Plant nutrition may also have an impact on the occurrence of russeting. Thus, according to Hao and Papadopoulos (2003), a high Ca-supply level ($300$ mg $L^{-1}$) reduced the incidence of fruit russeting in rockwool-grown tomatoes, compared with a low Ca treatment ($150$ mg $L^{-1}$). With respect to salinity, data reported by Sonneveld and van der Burg (1991) suggest an ameliorating effect of moderately high NaCl levels in the root zone (up to 25 mM) on the occurrence of russeting. A similar response was found by Chrétien *et al.* (2004).

Plants with a low fruit load and a high leaf to fruit ratio were reported to be more prone to fruit cuticle cracking (Bakker 1988; Bertin *et al.* 2000), while fruit pruning affects both the degree and severity of the disorder (Ehret *et al.* 1993). Demers *et al.* (2007) showed that russeting of greenhouse tomato was mostly influenced by the number of fruit per cluster (total fruit load), and very little by the number of leaves between clusters. Decreasing the number of fruit per cluster resulted in a progressive increase in the occurrence of russeting (Demers *et al.* 2007). Emmons and Scott (1997), however, were unable to induce fruit russeting by pruning leaves or fruit on tomato plants. Fruit size and fruit developmental stage also affect the degree and severity of cuticle cracking in the crop (Bakker 1988). As fruit size increased, the occurrence of cuticle cracking became more frequent (Hayman 1987; Emmons and Scott 1998; Dorais *et al.* 2004).

Microscopic inspection of the shoulder check roughness by Huang and Snapp (2004a) revealed many microscopic cracks that occurred in parallel lines. However, unlike russeting, which consists of randomly oriented cracks confined to the surface of the epidermis, shoulder check cracks were oriented parallel to each other and were not only confined to the cuticle but penetrated the epidermis. Shoulder check cracks also differed clearly from radial cracks, both in orientation and size. As in other types of fruit cracking, shoulder check crack appears mainly as a result of abrupt changes in soil moisture status, for instance when hot and dry weather is followed by precipitation in field tomato crops (Huang and Snapp 2004a). As reported by these authors, an enhanced boron supply (B foliar spray at $300$ mg $L^{-1}$) was associated with a less frequent incidence of shoulder check crack. In another experiment, weekly sprays with a $CaCl_2$ solution (50 mM Ca) consistently reduced fruit-cracking incidence to a moderate degree (Huang and Snapp 2004b). A combination of both treatments (Ca+B sprays at the above concentrations) further restricted the incidence of shoulder check crack in tomato fruits.

## *Oedema*

Oedema appears initially as pale-green or water-soaked blisters or bumps, which develop primarily on the undersides of leaves. In tomato, this physiological disorder is ascribed to a faster translocation of water to leaf tissues than the rate of removal via transpiration. Initially, the excess water causes swellings in certain areas of the leaf tissues, which may subsequently erupt (Grimbly 1986). As a result, yellow, brown, brownish-red, or even black spots may develop on the underside of leaves or veins, which in most cases have a crusty or corky appearance. As reported by Peet (2005), this physiological disorder is often mistaken for bacterial or fungal rust. Older leaves are more susceptible to this disorder than younger ones. Oedema is more likely to occur if excess water is delivered to plants via irrigation during periods of high air humidity and low irradiance (Sagi and Rylski 1978). A combination of high moisture levels in both the root zone and the air with low air temperatures provides ideal conditions for the occurrence of oedema, especially if susceptible cultivars are used. Efficient irrigation schedules based on the weather conditions and crop water demand may effectively prevent the occurrence of this disorder in greenhouse tomato crops. If the disorder is detected in the greenhouse, measures that increase the transpiration rate, such as ventilation or an increase in the heating temperature, may considerably reduce the incidence of oedema.

## Pepper

### *Blossom-end rot*

Pepper is susceptible to blossom-end rot. As in tomato, the incidence of BER in pepper (**Plate 2D**) is ascribed to a local deficiency of Ca in the distal part of the fruit during the initial stages of its development (Heuvelink and Körner 2001). In most cases, BER occurs close to the distal end of the fruit. However, in contrast to tomato, BER in pepper is rarely actually located at the blossom-end (Bosland and Votava 2000). In most cases, environmental conditions such as low air RH and high temperature, as well as fertilization and irrigation management, may restrict the translocation of Ca to a certain part of the fruit (Taylor and Locascio 2004; Bar-Tal *et al.* 2006; Savvas *et al.* 2007). As a result, a local Ca shortage may occur, which results in cell membrane disorganization and subsequent rotting (Bosland and Votava 2000; Taylor and Locascio 2004). In agreement with the above reports, Katsoulas *et al.* (2007) found a significantly lower incidence of BER in a pepper crop grown from June to November when the RH in the greenhouse during summer was maintained at 80% by means of a fog system, in comparison with no application of fog (**Fig. 3**). As reported by Prieto *et al.* (2007), BER in pepper appears mainly during the season of increasing day length, from early spring to summer, whereas in the season of decreasing photoperiod, progressing from early autumn to winter, BER is rare.

Overall, higher salt concentrations than normal in the root environment may increase the incidence of BER in pepper (Navarro *et al.* 2002; Savvas *et al.* 2007). This is true even if Ca is one of the ions contributing to the high salt concentration in the root zone (Sonneveld and Van der Burg 1991; Savvas *et al.* 2007). In a study with NaCl- or nutrient-induced salinity in the range 2.5-5.2 dS $m^{-1}$, Sonneveld and van der Burg (1991) found that a rise of the EC in the root zone significantly increased the incidence of BER in sweet pepper. The increase of EC by adding NaCl to the nutrient solution had a more pronounced effect than nutrient-induced salinity on BER in peppers. Silber *et al.* (2005) found that a high irrigation frequency may appreciably restrict the occurrence of BER. However, according to Savvas *et al.* (2007), a high irrigation frequency restricts BER only in crops not exposed to NaCl-salinity, while at high salt levels in the root zone a more frequent irrigation schedule is incapable of restricting this physiological disorder (**Fig. 4**). De Kreij (1999) concluded that the incidence of BER in pepper is primarily influenced by the cation ratios in the root environment, when the total ionic concentration is within the standard range for this crop species (EC 1-3 dS $m^{-1}$). Specifically, the occurrence of BER in sweet pepper

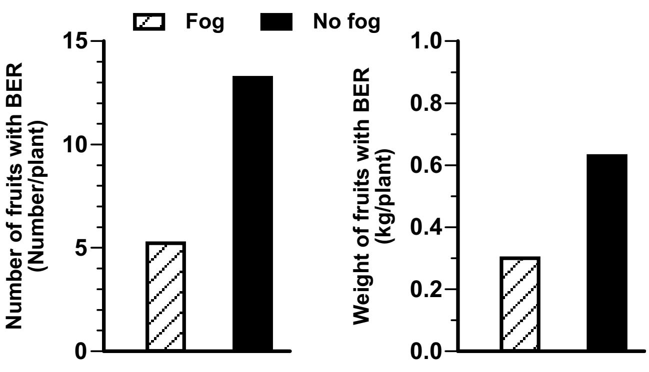


**Fig. 3 The incidence of blossom-end rot (BER) in pepper fruit as influenced by the use of a fog system to control air temperature and humidity in a greenhouse under Mediterranean summer conditions.** Based on data originating from **Katsoulas N, Kittas C, Tsirogiannis IL, Kitta E, Savvas D** (2007) Greenhouse microclimate and soilless pepper crop production and quality as affected by a fog evaporative cooling system. *Transactions of the American Society of Agricultural and Biological Engineers* **50**, 1831-1840, with kind permission from the ASABE, ©2007.

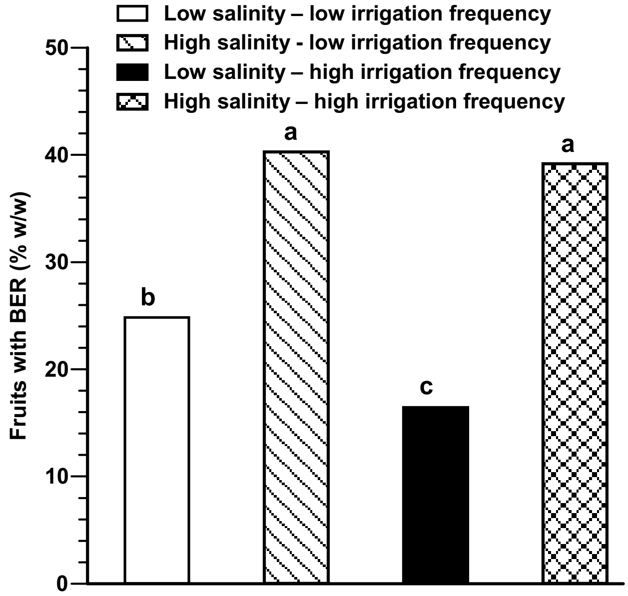


**Fig. 4** Influence of irrigation water salinity (S) and irrigation frequency (IF) on the incidence of blossom-end rot (BER) in a pepper crop grown hydroponically. Based on data from **Savvas D, Stamati E, Tsirogiannis IL, Mantzos N, Barouchas PE, Kittas K, Katsoulas N** (2007) Interactions between salinity and irrigation frequency in greenhouse pepper grown in a closed-loop hydroponic system. *Agricultural Water Management* **91**, 102-111, with kind permission from Elsevier, ©2007.

fruit is promoted by a high K: Ca ratio in the root environment.

Marcelis and Ho (1999) noticed that both the growth rate of young pepper fruits and the incidence of BER increased with the number of seeds per fruit. Furthermore, these researchers observed that the Ca concentration of the pericarp in mature pepper fruit was negatively related to both fruit size and BER incidence. Based on these findings, Marcelis and Ho (1999) suggest that a Ca shortage becomes more likely under conditions of rapid growth due to a higher rate of Ca utilization than Ca delivery, which results in cell membrane impairment manifested as BER. Nevertheless, Turhan *et al.* (2006b) found that pepper fruits grown in a ventilated-cooled greenhouse had a higher initial growth rate than those grown in a non-cooled greenhouse and this was associated with a lower incidence of BER. According to these authors, the occurrence of BER in pepper fruits is associated with impaired sucrose metabolism in fruit tissues, which may reduce growth rates and final size.

An increase of the $NH_4$ concentration in the nutrient solution supplied to pepper may decrease the uptake of Ca by the plant, thereby raising the incidence of BER (Bar Tal *et al.* 2001a). Recently, a shortage of Mn in affected tissues has been also implicated in the occurrence of BER in pepper fruit (Silber *et al.* 2005; Turhan *et al.* 2006a). According to these authors, a low Mn level may be associated with an increase in NAD(P)H oxidase activity in the pericarp of pepper fruit, which enhances the production of reactive oxygen species in the apoplast (Aktas *et al.* 2005). As a result, membrane integrity may be subjected to oxidative damage, especially if the enhanced production of reactive oxygen species is accompanied by a temporary Ca shortage.

### *Fruit cracking*

Fruit cracking is one of the most serious problems in commercial sweet pepper crops due to its detrimental effect on product quality (Yao *et al.* 2000). Depending on the extent of cracks, affected fruits may be graded either Class II or non-marketable (EU, Commission Regulation No. 1455/1999). Similarly to tomato, cracking of pepper fruits may be classified as radial, concentric, or cracking of the cuticle. Of these types, cuticular cracking, which is sometimes referred to as russeting, is the most serious problem in greenhouse pepper crops. Under greenhouse conditions, fruit become susceptible to cracking at the stage of colour change (Aloni *et al.* 1999).

Scanning-electron micrographs have shown that fruit cracking in pepper is initiated by the formation of mini-cracks in the cuticle layer, which gradually enlarge into cracks and traverse the epidermal cells (Aloni *et al.* 1998). Repeated shrinkage and expansion of the fruit due to large diurnal fluctuations in fruit turgor weakens the fruit cuticle and exacerbates cracking (Aloni *et al.* 1999; Yao *et al.* 2000). Pepper cultivars differ in their susceptibility to produce cracked fruits, partly because of differences in fruit pericarp thickness. According to Moreshet *et al.* (1999), pepper fruit with a high expansion-shrinkage amplitude show more severe cracking symptoms.

Restriction of night transpiration under low air temperatures and high RH, which increases cell turgor in the fruit pericarp, is generally implicated as the most prominent factor in the occurrence of fruit cracking in pepper (Aloni *et al.* 1998; Moreshet *et al.* 1999). This was clearly demonstrated by Moreshet *et al.* (1999) in an experiment conducted in two greenhouses, which differed in the night humidity regimes. As reported by these authors, the percentage of cracked pepper fruit was significantly higher in the greenhouse with a low VPD during the night than in that with a high VPD (low RH). Similarly, leaf pruning, which also restricts night transpiration, caused a significant increase in pepper fruit cracking (Aloni *et al.* 1998). These results indicate that the factors promoting the incidence of fruit cracking are those restricting the occurrence of BER. Therefore, fruit cracking occurs mainly in the winter, when transpiration rates during the night are very low, while BER affects pepper fruit mainly in spring and summer, when night temperatures and transpiration rates increase (Bar-Tal *et al.* 2006). There is hardly any information regarding the involvement of Ca in the occurrence of pepper fruit cracking. However, since cuticle cracking also depends on the resistance of the cell walls and/or membranes to excessive turgor pressure, and this may be influenced by the local Ca status, Ca is still likely to be implicated in fruit cracking in pepper.

Because the water status of the fruit is a key factor in determining the severity of fruit cracking, this disorder is not only influenced by the night but also by the daily rates of water intake and transpiration. Thus, when an evaporative cooling system was used in a greenhouse pepper crop to raise the air RH during the day and thereby reduced transpiration rates, the incidence of cracked fruits increased (Bar-Tal *et al.* 2006). Furthermore, under conditions of less frequent irrigation and/or increased solar radiation, which decrease air RH and enhance transpiration, the incidence of fruit cracking decreased (Jovicich *et al*. 2007). Moderate increase of salt concentration in the root environment of hydroponically-grown pepper seems to reduce the incidence of russeting in fruit (Sonneveld and van der Burg 1991).

### *Colour spots and flecks*

There are several terms in the literature referring to colour spots or flecks in pepper fruit. Thus, in some papers the term ‘white flecks’ (de Kreij 1995) is used, while in other publications a disorder characterized as ‘green spots’ is referred to (Sonneveld and Van der Burg 1991; de Kreij 1995; Bosland and Votava 2000). Jovicich *et al*. (2007) used the term ‘yellow spots’ to describe a colour disorder of the pepper fruit. Furthermore, Smith *et al*. (1996) described a physiological disorder called ‘stip’ or ‘black spot’, which is manifested as grey-brown to greenish spots either on the fruit surface or internally within the fruit tissue. It is not quite clear if these terms are used as synonyms to describe the same disorder or if they refer to distinct disorders with a different aetiology. Unfortunately, the information available concerning the appearance of colour spots in pepper is limited. Therefore, the causes of this disorder and the conditions that promote its occurrence are still unclear.

As suggested by Aloni *et al.* (1994), the occurrence of colour spots in pepper is strongly influenced by the rate of nitrogen fertilization and the operations aimed at reducing the solar radiation intensity (shading). According to Sonneveld and van der Burg (1991) and de Kreij (1995), an increased nutrient solution EC restricts the incidence of white flecks and green spot. In agreement with this, Jovicich *et al.* (2007) found a lower incidence of yellow spots in pepper fruit as the nutrient solution strength increased and the frequency of irrigation decreased. These results may indicate that the terms ‘white flecks’, ‘green spots’ and ‘yellow spots’ are different nuances of the same disorder, which is favoured by a high water potential in the root zone. It is not clear if Ca is related to the occurrence of this disorder.

As stated by Bosland and Votava (2000), the occurrence of stip or black spot is favoured by the advent of cooler temperatures and shorter days after a period of normal fruit growth. It seems that stip is a Ca-related physiological disorder which mainly affects some susceptible cultivars.

### *Oedema*

Pepper leaves may be affected by oedema (Bosland and Votava 2000), the symptoms and aetiology of which are similar to those already described for tomato. In pepper plants, oedema may appear not only on the underside of lamina but also on the petiole.

### *Abortion of the reproductive organs*

A physiological disturbance that may adversely affect the total fruit yield of pepper is the abortion of buds, flowers and immature fruit. Several factors may be involved in the occurrence of this disorder, including heat stress, low solar radiation, insufficient nutrient and/or water supply or excessive fertilization (Bosland and Votava 2000). According to Marcelis *et al*. (2004), flower and fruit abortion may be caused by any factor that disturbs the equilibrium between source and sink, either by decreasing the source capacity or by increasing the sink demand, or by both. Hence, any measure aimed at maintaining or re-establishing the source to sink equilibrium is more or less effective in controlling the abortion of buds, flowers and immature fruit.

## Eggplant

### *Blossom-end rot*

Blossom-end rot also affects eggplant (Taylor and Locascio 2004), which usually begins as a small water-soaked area at the blossom-end of the fruit that subsequently develops into a dry rot. However, eggplant is appreciably less susceptible to BER than tomato or sweet pepper. A recent screening of commercial eggplant cultivars and landraces performed by Raigon *et al.* (2008) revealed a very low incidence of BER in all of the tested commercial hybrids and relatively high Ca levels within the fruit. These results support the hypothesis that BER is related to the Ca concentration in the fruit. Raigon *et al*. (2008) ascribed the low susceptibility of eggplant to BER to the fact that commercial varieties have been subjected to selection for the low incidence of this physiological disorder.

### *Internal fruit rot*

Internal fruit rot (IFR) is another physiological disorder that was reported to affect eggplant fruits (de Kreij 1990; Savvas and Lenz 1994). The early symptom of this disorder is the appearance of an uneven, wet area on the external fruit surface, which is localized mainly in the distal region (Savvas and Lenz 1994). Below this uneven area, the fruit tissue appears wet, blackened and disintegrated, presumably as a result of cell bursting and disorganization (**Plate 2E**). The dark colour of the disintegrated tissue apparently originates

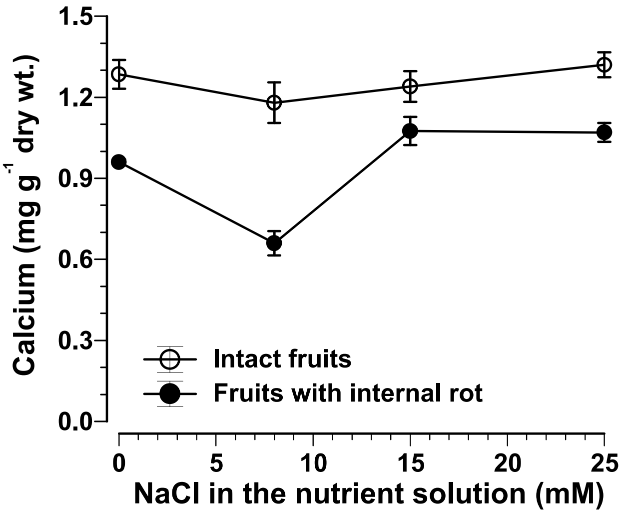


**Fig. 5 Calcium concentrations in eggplant fruits with and without internal fruit rot (IFR) originating from plants grown at four different NaCl-salinity levels.** Reproduced from **Savvas D, Lenz F** (1994) Influence of salinity on the incidence of the physiological disorder "internal fruit rot" in hydroponically grown eggplants. *Angewandte Botanik* **68**, 32-35, with kind permission from the Vereinigung für Angewandte Botanik, ©1994.

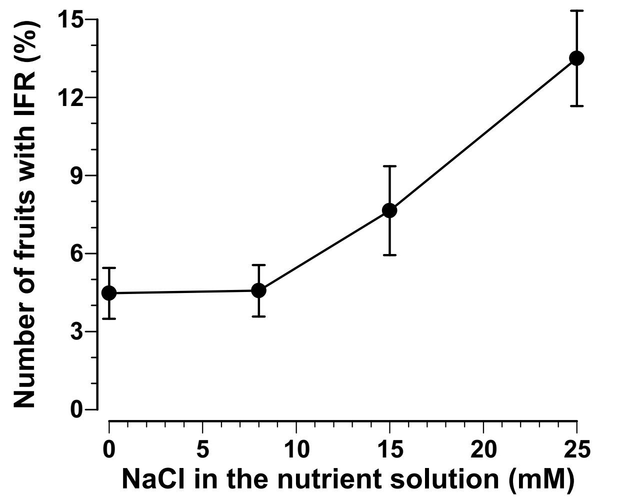


**Fig. 6 The effect of NaCl concentration in the root zone on the incidence of internal fruit rot (IFR) in eggplant grown in a recirculating nutrient solution.** Based on data originating from **Savvas D, Lenz F** (1994) Influence of salinity on the incidence of the physiological disorder "internal fruit rot" in hydroponically grown eggplants. *Angewandte Botanik* **68**, 32-35, with kind permission from the Vereinigung für Angewandte Botanik, ©1994.

from the oxidation of constituents released from the disorganized cells. At a latter stage, the fruit skin may crack and a black juice may be excreted.

Internal fruit rot seems to be a calcium-related physiological disorder, caused by similar factors to those implicated in the occurrence of BER in tomato and pepper (de Kreij 1990). In an experiment with eggplants exposed to different levels of NaCl-salinity, Savvas and Lenz (1994) found that the Ca concentrations in eggplant fruit affected by IFR were always lower than those in intact fruits at all salinity levels, although the increase of the external NaCl concentration up to 25 mM did not affect the fruit Ca concentration (**Fig. 5**). Furthermore, it was shown that the exposure of plants to NaCl salinity aggravated the incidence of IFR (**Fig. 6**). In two other experiments with eggplants, it was found that the impact of nutrient-induced salinity on the occurrence of IFR was similar with that of NaCl-salinity maintained at the same EC (Savvas 1992).

## CONCLUSIONS AND FUTURE PERSPECTIVES

Plant nutrition in relation to growth and development continues to be a major area of study in horticultural crops. With increasing knowledge of the importance of fruit components, such as antioxidants and vitamins, for human health greater emphasis is now placed on the nutritive value of produce, as well as on the molecular basis of mechanisms implicated in the uptake and utilization of inorganic nutrients by the plants. In a comparative review of the Solanaceae, it is inevitable that given its greater importance as a crop, tomato has been researched much more than pepper or eggplant. Particularly in the case of eggplant, there are still many areas of plant nutrition and fruit quality that lack information. However, given its importance as a virtual staple food in some countries, coupled to its high antioxidant value, eggplant is attracting increasing attention and a greater research input on this species may be expected over the coming years.

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