Nitrogen Nutrition of Greenhouse Pepper. I. Effects of Nitrogen Concentration and $\text{NO}_3 : \text{NH}_4$ Ratio on Yield, Fruit Shape, and the Incidence of Blossom-end Rot in Relation to Plant Mineral Composition

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Abstract. Blossom-end rot (BER) is one of the major physiological disorders of greenhouse bell pepper (*Capsicum annuum* L.). The objective of the present work was to study the effects of the solution N concentration and $\text{N-NO}_3 : \text{N-NH}_4$ ratio on fruit yield and the incidence of BER and other fruit-quality traits of greenhouse-grown bell pepper in a Mediterranean climate. Three experiments were conducted: Expt. 1 included five total N concentrations (0.25 to 14 $\text{mmol}\cdot\text{L}^{-1}$, with a constant $\text{N-NO}_3 : \text{N-NH}_4$ ratio of 4); Expt. 2 included five treatments of different $\text{NO}_3 : \text{NH}_4$ molar ratios (0.25 to 4, with a constant N concentration of 7 $\text{mmol}\cdot\text{L}^{-1}$); and Expt. 3 included three treatments of different $\text{NO}_3 : \text{NH}_4$ molar ratios (1.0, 3.0 and 9.0, with a constant N concentration of 7 $\text{mmol}\cdot\text{L}^{-1}$). Plants were grown in an aero-hydroponics system in Expts. 1 and 2 and in tuff medium in Expt. 3, in greenhouses in Israel. The optimal values of N concentration for total fruit yield and for high fruit quality (marketable) were 9.3 and 8.3 $\text{mmol}\cdot\text{L}^{-1}$, respectively. The total and high-quality fruit yields both increased with increasing $\text{N-NO}_3 : \text{N-NH}_4$ ratio in the range studied. The total and high-quality fruit yields both decreased sharply as the NH_4 concentration in the solution increased above 2 $\text{mmol}\cdot\text{L}^{-1}$. The increase in the NH_4 concentration in the solution is the main cause of the suppression of Ca concentration in the leaves and fruits and the increased incidence of BER. The occurrence of flat fruits also increased with increasing NH_4 concentration in the solution.

Bell pepper fruit quality in Israeli commercial and experimental greenhouses decreases during spring and summer, because of blossom-end rot (BER) and shape deformation of fruits (Israel Ministry of Agriculture, unpublished data). A $\text{N-NO}_3 : \text{N-NH}_4$ ratio of 1:1 was found to be optimal for growth of young tomato plants under a wide range of root temperatures (Ganmore-Neumann and Kafkafi, 1980a). Feigin et al. (1980) reported that the solution NH_4 fraction in the range of 0% to 30% had no signifi-

cant effect on fruit yield of tomato, but the yield decreased as the NH_4 fraction increased from 30% to 50%. In the Netherlands, the recommended $\text{N-NO}_3 : \text{N-NH}_4$ ratio for greenhouse bell pepper is much higher, $\approx 6:1$ (Roorda van Eysinga and van der Meijs, 1981). The $\text{N-NO}_3 : \text{N-NH}_4$ ratio affects BER, probably because of its effects on Ca uptake and concentration in tomato (Wilcox et al., 1973; Wojciechowski et al., 1969) and bell pepper (Marti and Mills, 1991; Morley et al., 1993) fruit. The early stage of fruit development is the period of greatest sensitivity to Ca supply (Marcelis and Ho, 1999; Marti and Mills, 1991). Recently, Marcelis and Ho (1999) showed that the incidence of BER in pepper correlated well with the Ca concentration in the fruit. Ho et al. (1993) reported that high radiation combined with NH_4 nutrition increased the incidence of BER in tomato. There is a lack of quantitative information on the effect of NH_4 concentration on BER in greenhouse-grown pepper under spring and summer conditions in a Mediterranean climate.

Fruit deformation is another widespread disorder affecting bell pepper production,

especially during the springtime and onward. One of the deformations is that the fruits are flat instead of having the desired blocky shape, with a length/diameter ratio of 1.0. Flat fruits are defined here as fruits with a length/diameter ratio below 0.90 but above 0.8. This disorder is distinct from the disorder which causes very flat seedless fruits; the flat fruits described here have a normal number of seeds; therefore this physiological disorder is not related to the absence of seeds. It is well known that the final shape of the fruit is strongly affected by pre-anthesis temperature conditions (Ali and Kelly, 1993; Aloni et al., 1999; Polowick and Sawhney, 1985; Rylski, 1973; Rylski and Spigelman, 1982). Rylski and Spigelman (1982) reported that a low night temperature (12 °C) caused deformed, blunt pepper fruits. Aloni et al. (1999) reported that conditions that enhance carbohydrate accumulation in the flower increase the size of the ovary and the incidence of flat fruits in bell pepper. There is no information on the effect of plant nutrition on the incidence of flat fruits.

The objective of the present investigation was to study the effects of N concentration and the $\text{N-NO}_3 : \text{N-NH}_4$ ratio on fruit yield and quality, in relation to the mineral composition of the organs of greenhouse-grown bell peppers.

Materials and Methods

Plant growth and experimental design. Expts. 1 and 2. The experiments were conducted at Bet Dagan, Israel (35°E, 31°N; 50-m altitude), in a climate-controlled greenhouse. Minimum and maximum air temperatures were 18 and 30 °C, respectively. Bell pepper plants, cv. Mazurka, were grown in an aero-hydroponics system, as described by Feigin et al. (1984), consisting of two separate $50 \times 29 \times 20$ -cm deep polystyrene boxes mounted on a 140-L covered container (one plot). Roots were exposed continuously to the nutrient solutions that were circulated by means of a pump and plastic tube system with small holes through which the solution was injected. The solution was leached to the bottom of the 140-L container and recirculated. Expt. 1 included five total N levels, 0.25, 3.50, 7.0, 10.5, and 14.0 $\text{mmol}\cdot\text{L}^{-1}$ (with constant $\text{N-NO}_3 : \text{N-NH}_4$ ratio of 4:1) and Expt. 2 included five $\text{N-NO}_3 : \text{N-NH}_4$ ratios, 0.25, 0.50, 1.00, 2.00, and 4.00 (at a constant N concentration of 7.0 $\text{mmol}\cdot\text{L}^{-1}$) (Table 1). The treatment with $\text{N-NO}_3 : \text{N-NH}_4$ ratio of 4.00 was also included in Expt. 1. The only ions that varied among treatments, in addition to NH_4 and NO_3 , were Cl, SO_4 and protons (Table 1). In both experiments the nutrient solutions were prepared with tap water containing about (in $\text{mmol}\cdot\text{L}^{-1}$) 0.2 NO_3 , 4 Cl, 1.5 SO_4 , 1 HCO_3 , 2 Ca, 1 Mg, and 3.5 Na. The initial pH of the solution was 6.5 and it was monitored daily; when it increased above 7.0, sulfuric acid was added and when it fell below 6.0, sodium hydroxide was added to adjust the pH back to 6.5. The electrical conductivity (EC) was in the 2.0–2.5 $\text{dS}\cdot\text{m}^{-1}$

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Table 1. Composition of the nutrient solution in the three experiments.^z

Expt. 1. Increasing N at a constant N-NH ₄ : N-NO ₃ ratio of 4.0.								
N	NO ₃	NH ₄	NH ₄ NO ₃	HNO ₃	KNO ₃	KCl	Mg(NO ₃) ₂	MgSO ₄
	mmol·L ⁻¹							
0.25	0.20	0.05	0.0	0.0	0.0	5.0	0.0	1.0
3.5	2.80	0.70	0.7	0.0	2.1	2.9	0.0	1.0
7.0	5.60	1.40	1.4	0.0	4.2	0.8	0.0	1.0
10.5	8.40	2.10	2.1	1.3	5.0	0.0	0.0	1.0
14.0	11.20	2.80	2.8	1.3	5.0	0.0	1.0	0.0
Expt. 2. Increasing N-NO ₃ : N-NH ₄ ratio at a constant total N concentration of 7.0 mmol·L ⁻¹ .								
N-NO ₃ /N-NH ₄	NO ₃	NH ₄	NH ₄ NO ₃	KNO ₃	(NH ₄) ₂ SO ₄	KCl		
	mmol·L ⁻¹							
0.25	1.40	5.60	1.4	0.0	2.1	5.0		
0.50	2.33	4.66	2.3	0.0	1.15	5.0		
1.00	3.50	3.50	3.5	0.0	0.0	5.0		
2.00	4.66	2.33	2.3	2.3	0.0	2.7		
4.00	5.60	1.40	1.4	4.2	0.0	0.8		
Expt. 3. Increasing N-NO ₃ : N-NH ₄ ratio at a constant total N concentration of 7.0 mmol·L ⁻¹ .								
N-NO ₃ /N-NH ₄	NO ₃	NH ₄	NH ₄ NO ₃	HNO ₃	KNO ₃	KCl		
	mmol·L ⁻¹							
1.00	3.50	3.50	3.5	0.0	0.0	5.0		
2.00	4.66	2.33	2.3	0.0	2.3	2.7		
9.00	6.30	0.70	0.7	0.6	5.0	0.0		

^zIn the three experiments, all solutions contained 1.0 mmol·L⁻¹ H₃PO₄, 27.9 µmol·L⁻¹ Fe as Sequestin, 10.5 µmol·L⁻¹ Mn, 4.4 µmol·L⁻¹ Zn, 0.3 µmol·L⁻¹ Mo and 0.7 µmol·L⁻¹ Cu as EDTA chelates, and 40 µmol·L⁻¹ H₃BO₃. In Expts. 2 and 3 the solutions contained 1.0 mmol·L⁻¹ MgSO₄.

range (the addition of sulfuric acid or sodium hydroxide for pH adjustment did not increase the EC above 2.5 dS·m⁻¹). The nutrient solution was renewed every 2 weeks and the nutrient solution concentrations were determined. In that period of time the concentration of NH₄ declined much faster than that of NO₃, therefore, the concentrations of NH₄ and NO₃ were determined weekly; (NH₄)₂SO₄ and HNO₃ in the proper ratio were added weekly to adjust the N-NO₃ : N-NH₄ ratio and the total N concentration.

Pepper seedlings were grown in a commercial nursery until four true leaves developed, in seedlings trays (pyramid cells of 19.4 cm² area, 15 cm³ volume), in a 1 peat : 1 vermiculite (v/v) mixture. The seedlings were top irrigated with a solution containing fertilizer according to the best known procedure of the commercial nursery. Twelve uniform seedlings of four true leaves were transplanted in each plot on 31 Aug. 1995. Fifteen days after transplanting (DAT) four plants were thinned, and after 38 and 62 DAT two more

plants were removed, leaving the most uniform four plants in each plot (two plants/m², including area between the containers, until the termination of the experiments on 242 DAT). The treatments were arranged in five randomized blocks. The treatments, involving various solution compositions, started 31 DAT, except for those using N-NO₃ : N-NH₄ ratios of 0.5 and 0.25 that started at a ratio of 1.0 and changed to the final value at 138 and 151 DAT, respectively. The transition from a

ratio of 1.0 to 0.5 and to 0.25 was conducted gradually, to avoid a shock of ammonium toxicity before the production of fruits, which were the major focus of this study. Vertical threads and plastic rings supported two main plant stems; lateral branches were removed frequently. Red fruits (80% color) were harvested weekly from 78 DAT until the termination of the experiment, 242 DAT. Fruit number, physiological disorders (BER and flat fruits), fruit weight, total, and high quality yield were determined. High quality fruits were defined as those that were not affected by physiological disorders, deformed shape, discoloring, or cracks. At the end of the experiments, the plants were divided into root, stem, old leaves (up to five nodes above the branching into two main stems), young leaves (from the highest five nodes) and fruits. The fruits were divided among four developmental stages: young fruits (up to 3 cm in length), green fruits, half-red fruits (50% to 80% red) and red fruits. Samples of each plant part were analyzed for dry matter percentage and mineral composition (N, K, Ca, and Mg).

Expt. 3. Bell pepper plants (cv. Mazurka) were grown in red tuff (Scoria, from the Golan Heights, 0–8 mm equivalent diameter) medium. Tuff is a granulated volcanic material that formed as a result of violent eruptions and rapid cooling of ejected magma containing water vapor and other gases. It is widely used as a container medium in greenhouse horticulture due to its preferable physical characteristics relative to soil, high hydraulic conductivity, high air : water ratio under low tension and low density (Chen et

Table 2. Total and high quality fruit yield, BER incidence and the fruit length to diameter ratio as affected by the N-NO₃ : N-NH₄ ratio in the nutrient solution, Expt. 3. Dec. 1996 to June 1997.

NO ₃ /NH ₄	Total	High quality	BER	Length : diameter
	Yield	Yield		
molar ratio	— — —	t/ha ⁻¹ — — —	%	
1.0	144.8 a	67.1 a	22.7 a	0.959 a
3.0	148.2 a	63.2 b	27.3 b	0.941 b
9.0	130.4 b	49.5 c	32.4 c	0.913 c
LSD _{0.05}	1.67	1.69	1.26	0.0047
F prob.	<0.01	<0.01	<0.01	<0.01

Fig. 1. Total (■) and high-quality (□) fruit yields as a function of total N concentration (N-NO₃ : N-NH₄ ratio of 4.0, Expt. 1, 30 Apr. 1996) and as a function of N-NO₃ : N-NH₄ ratio (at total N concentration of 7 mmol·L⁻¹, Expt. 2, 30 Apr. 1996). The lines for Expts. 1 and 2 are the best-fitted quadratic regressions. Error bars are SE.

Fig. 2. The effects of total N concentration (at N-NO₃ : N-NH₄ ratio of 4.0, Expt. 1, Apr. 1996) and N-NO₃ : N-NH₄ ratio (at total N concentration of 7 mmol·L⁻¹, Expt. 2, Apr. 1996) on the occurrence of blossom end rot (□) and the occurrence of flat fruits (▲). The lines for BER and flat fruit for Expts. 1 and 2 are the best-fitted regressions. Error bars are SE.

al., 1980; Galin and Singer, 1988; Wallach et al. 1992). The experiment included three treatments of differing N-NO₃ : N-NH₄ ratios: 1.0, 3.0 and 9.0 (all with N concentration of 7.0 mmol·L⁻¹). In order to obtain 1 mm P and 5 mm K, and the desired N-NO₃ : N-NH₄ ratios different combinations of salts were used as given in Table 1. Microelements were also added as salts in similar concentrations to those used in Expts. 1 and 2. These fertilizers were injected into the irrigation water, which contained ≈0.5 mm NO₃, 4 mm Cl, 2 mm H₂CO₃, 1.5 mm SO₄, 1.5 mm Ca, 1 mm Mg, and 3.5 mm Na. The pH of the irrigation solution was kept at 6.0 by adding sulfuric acid. The electrical conductivity (EC) of the irrigation and drainage water was in the range of, 1.5–2.0 and 2.5–3.0 dS·m⁻¹, respectively. When the EC of the drainage water increased to 3.0 dS·m⁻¹, additional irrigation water without fertilizer was applied to reduce the EC.

The experiment was arranged in four randomized blocks, each plot included six containers per row. Each container (50 cm width, 100 cm length and 20 cm depth, 100 L volume) contained tuff medium; the distance between row centers was 1.8 m, and plant density on the ground was 3.3 plants/m². Six plants were grown in two rows in each container, i.e., 36 plants per plot. The nutrient solutions were applied by means of 2.4 L·h⁻¹ drippers, 30 cm between drippers, one line per row. Seedlings from the same nursery as in experiments 1 and 2, with four true leaves were transplanted on 25 Aug. 1996 and the experiment was terminated on 8 June 1997. The experiment was conducted in the Lachish Experimental Station, Israel (36°E, 30°N; 100-m altitude), in a partly climate-controlled greenhouse, equipped with ventilators, side curtains and a heater. The minimum air temperature was set to 18 °C, and the maximum temperature ranged from 18 °C in January and February to 40 °C in May and June. Vertical threads and plastic rings supported two main plant stems; lateral branches were removed frequently as in Expts. 1 and 2. Red fruits were harvested from 99 DAT to the termination of the experiment, 287 DAT. Fruit number, weight, and physiological dis-

orders were determined as in Expts. 1 and 2. Samples of old and young leaves and pepper fruits at the termination of the experiment were analyzed to determine dry matter percentage (dried at 60 °C) and mineral composition. Fruits of different developmental stages were picked on the last sampling date and each fruit was divided into three parts: distal, medium, and the blossom end.

Mineral analysis. Potassium, Ca, and Mg analyses of plant organs were carried out after digestion of ground dry samples with nitric acid and perchlorate. Potassium concentration was determined by flame photometry and Ca and Mg concentrations by atomic absorption spectrophotometer. Nitrogen analysis (all N except nitrate and nitrite) of plant organs was carried out after digestion

Table 3. Mineral composition of plant organs at the termination of Expt. 1 (30.04.96) as affected by N concentration (N-NO₃ : N-NH₄ = 4.0) in the nutrient solution.

N	Ca	Mg	K	N	Ca	Mg	K	N
mmol·L ⁻¹		mg·g ⁻¹				mg·g ⁻¹		
		Stem				Root		
0.25	5.7	3.7	27.2	9.6	8.7	2.8	24.8	42.8
3.50	5.8	4.2	26.6	13.0	11.0	3.4	30.8	63.4
7.00	5.5	4.3	25.4	23.3	6.7	3.0	25.9	64.8
10.50	5.4	4.6	26.1	26.0	7.2	3.2	27.2	68.8
14.00	5.5	4.5	26.5	30.8	4.4	2.4	14.8	60.4
LSD _{0.05}	0.2	0.2	1.5	2.5	0.5	0.1	0.8	2.3
F prob.	NS	0.055	NS	<0.0001	<0.0001	0.0005	<0.0001	<0.0001
		Old leaves				Young leaves		
0.25	39.0	16.9	41.4	25.8	18.4	10.3	59.2	39.4
3.50	34.0	16.2	56.8	39.8	20.2	8.8	55.8	61.6
7.00	30.3	15.6	76.0	45.8	15.8	7.8	52.8	64.3
10.50	26.0	12.0	72.4	45.8	16.7	7.9	57.2	68.8
14.00	27.0	12.7	71.8	48.6	19.0	8.5	54.6	68.2
LSD _{0.05}	0.8	0.4	2.3	2.2	0.8	0.4	2.3	2.2
F prob.	<0.0001	<0.0001	<0.0001	<0.0001	<0.005	0.0001	NS	<0.0001
Fruits at different developmental stages								
N	Ca	Mg	K	N				
mmol·L ⁻¹		mg·g ⁻¹						
		Average age						
0.25	0.88	2.77	54.5	26.0				
3.50	0.97	2.43	42.7	33.1				
7.00	0.85	2.33	41.3	36.1				
10.50	0.88	2.33	40.7	35.9				
14.00	0.72	2.12	35.3	37.7				
LSD _{0.05}	0.05	0.07	1.5	1.3				
Stage		Average N treatments						
Young	1.18	3.03	50.6	41.8				
Green	0.94	2.29	45.6	34.0				
Half red	0.67	2.22	38.5	28.6				
Red	0.65	2.04	37.1	30.7				
LSD _{0.05}	0.04	0.06	1.2	1.1				
Analysis of variance (F probability)								
N	0.002	<0.0001	<0.0001	<0.0001				
Stage	0.0001	<0.0001	<0.0001	<0.0001				
Block	0.032	NS	NS	NS				
N × stage	0.020	0.004	0.037	NS				

NS Nonsignificant.

Fig. 3. Effect of NH_4 concentration on total fruit yield ($\square, \blacklozenge$) and high quality fruit yield ($\triangle, \bullet$). The empty symbols are for Expt. 1 (N varied from 0.25 to 14.00 $\text{mmol}\cdot\text{L}^{-1}$) and the full symbols are for Expt. 2 ($\blacksquare, \bullet$) and Expt. 3 ($\blacklozenge, \blacktriangle$) (constant N, 7.0 $\text{mmol}\cdot\text{L}^{-1}$). The lines for total yield (continuous) and for high quality yield (dashed) in Expts. 1 and 2 are the best fitted linear regressions (for NH_4 concentration above 1 $\text{mmol}\cdot\text{L}^{-1}$) and the lines for Expt. 3 were drawn through the data points. Error bars are SE.

with sulfuric acid and peroxide and the ammonium concentration obtained was determined by Autoanalyzer (Lachat Instruments, Milwaukee, Wis.).

Statistics. The statistical analysis was carried out with the JMP software package (SAS Institute, Cary, N.C.) for the analysis of variance (ANOVA) of minerals concentrations in plant organs of all experiments and fruit yield,

high quality yield, BER, and flat fruit occurrence in Expt. 3. Linear and quadratic regressions and the NLIN procedure of that software were used to obtain the relations between solution N or NH_4 concentration and fruit yield, high quality yield, BER, and flat fruit occurrence in Expts. 1 and 2, and the correlation procedure were used for correlating BER with Ca concentrations in plant organs.

Table 4. Mineral composition of plant organs at the termination of Expt. 2 (30.04.96) as affected by NO_3^- : NH_4^+ ratio (N = 7 $\text{mmol}\cdot\text{L}^{-1}$) in the nutrient solution.

NO ₃ /NH ₄	Ca	Mg	K	N	Ca	Mg	K	N
molar ratio	mg·g ⁻¹				mg·g ⁻¹			
	Stem				Root			
0.25	5.1	5.5	21.9	35.3	4.0	2.3	14.8	57.3
0.50	5.0	5.2	22.2	34.4	4.6	2.4	14.6	62.4
1.00	5.3	4.9	25.9	31.8	4.7	2.3	14.0	63.0
2.00	5.3	4.5	26.5	27.4	6.3	3.0	26.1	67.2
4.00	5.5	4.3	25.4	23.3	6.7	3.0	25.9	64.8
LSD _{0.05}	0.17	0.28	0.9	0.8	0.3	0.1	1.8	3.8
F prob.	NS	0.046	0.010	<0.0001	<0.0001	0.0005	<0.0001	NS
	Old leaves				Young leaves			
0.25	23.8	11.5	61.8	50.3	14.3	7.0	43.8	71.8
0.50	25.8	12.6	60.2	49.0	16.5	8.3	47.0	70.8
1.00	20.5	9.8	69.3	45.3	14.4	6.9	56.0	66.5
2.00	29.7	14.5	68.6	44.4	16.6	8.4	54.2	69.8
4.00	30.3	15.6	76.0	45.8	15.8	7.8	52.8	64.3
LSD _{0.05}	0.8	0.4	2.3	2.2	0.8	0.4	5.0	2.2
F prob.	0.0001	0.0002	0.039	NS	0.039	NS	NS	0.005
Fruits at different developmental stages								
NO ₃ /NH ₄	Ca	Mg	K	N				
molar ratio	mg·g ⁻¹							
	Average ages							
0.25	0.70	1.89	33.7	37.6				
0.50	0.85	2.06	35.9	36.4				
1.00	0.76	2.07	37.3	36.9				
2.00	0.84	2.31	40.2	37.0				
4.00	0.85	2.38	41.5	36.5				
LSD _{0.05}	0.06	0.12	1.5	1.5				
Stage	Average NO ₃ /NH ₄ treatments							
Young	1.02	2.66	41.7	41.9				
Green	0.86	2.00	38.9	37.4				
Half red	0.69	2.00	34.0	32.9				
Red	0.63	1.91	36.3	35.4				
LSD _{0.05}	0.04	0.08	1.1	1.0				
Analysis of variance (F probability)								
NO ₃ /NH ₄	NS		0.0035	0.0004	NS			
Stage	<0.0001		<0.0001	<0.0001	<0.0001			
Block	NS		NS	NS	NS			
NO ₃ /NH ₄ × stage	NS		NS	NS	NS			

^{ns}Nonsignificant.

Results

Fruit yield and quality. The solution N concentration had a quadratic effect on total and high-quality fruit yield (Fig. 1). Raising the solution N concentration from 0.25 to 7 $\text{mmol}\cdot\text{L}^{-1}$ resulted in increases of high-quality and total yield by 350% and 550%, respectively. A further increase of the solution N concentration from 7 to 14 $\text{mmol}\cdot\text{L}^{-1}$ reduced the high-quality yield by 32%. The calculated N concentration for maximum yield was 9.4 $\text{mmol}\cdot\text{L}^{-1}$, coinciding with that for maximum leaf mass (Bar-Tal et al 2001). This value is within the range obtained by Aloni et al. (1994) for different open field cultivars fertilized as recommended. The calculated optimum for high quality yield was lower, at 8.3 $\text{mmol}\cdot\text{L}^{-1}$, probably because of the effect of NH_4 on the incidence of BER and flat fruit.

The solution N-NO_3^- : N-NH_4^+ ratio had a quadratic effect on total and high-quality fruit yield (Fig. 1). The increase in total and high-quality fruit yields was sharp as the N-NO_3^- : N-NH_4^+ ratio increased from 0.25 to 2.0, whereas the effect was smaller in the range of 2.0 to 4.0. The slope for high-quality yield was much steeper than that for total yields (Fig. 1a). The increase in total yield with the increasing N-NO_3^- : N-NH_4^+ ratio resulted mainly from the reduction of fruit physiological disorders, which reduced fruit mean weight. Extending the maximal N-NO_3^- : N-NH_4^+ ratio from 4:1 in Expt. 2 to 9:1 in Expt. 3, increased the yield of high quality fruit, but had no significant effect on the total yield (Table 2).

The solution N concentration in the range of 0.25 to 7 $\text{mmol}\cdot\text{L}^{-1}$ had no effect on the incidence of BER, but as the N concentration increased from 7.0 to 10.5 $\text{mmol}\cdot\text{L}^{-1}$ the incidence of BER increased significantly and a further increase to 14 $\text{mmol}\cdot\text{L}^{-1}$ had no effect (Fig. 2). This pattern was best described by a polynomial curve of the third order.

The N-NO_3^- : N-NH_4^+ ratio had a quadratic effect on the incidence of BER (Expt. 2, Fig. 2). Changing the ratio from 0.25:1 to 2:1 had only a slight effect on the incidence of BER, but a further increase to 4:1 reduced it sharply (Expt. 2, Fig. 2). A further increase of the N-NO_3^- : N-NH_4^+ ratio from 3:1 to 9:1 (Expt. 3) resulted in a significant reduction of the incidence of BER (Table 2).

The solution N concentration had a strong influence on the formation of flat fruits: the incidence of flat fruits increased linearly with increasing total N concentration through the studied range of 0.25 to 14.0 $\text{mmol}\cdot\text{L}^{-1}$ (Expt. 1, Fig. 2).

The N-NO_3^- : N-NH_4^+ ratio had a quadratic effect on the incidence of flat fruits; increasing the ratio from 0.25:1 to 2:1 caused a steep reduction in the incidence of flat fruits, whereas a further increase in the ratio to 4:1 had small effect (Expt. 2, Fig. 2). Increasing the ratio from 3:1 to 9:1 caused a further reduction in the fruit length to width ratio (Table 2).

Mineral composition of plant organs. The N concentration in all plant organs increased significantly as the solution N concentration

increased from 0.25 to 14.0 mmol·L⁻¹ at a constant N-NO₃:N-NH₄ ratio of 4.0 (Expt. 1, Table 3). The N concentration was higher in young leaves than in old leaves, possibly because of translocation of N from old to young leaves. Fruit N concentration declined with fruit development.

The N concentration in the stem and leaves declined as the N-NO₃:N-NH₄ ratio increased from 0.25:1 to 4:1 (Expt. 2, Table 4). A further increase of this ratio from 3:1 to 9:1 resulted in decline of N concentration in the stem and leaves and fruits (Expt. 3, Table 5).

The observed variation among plant organs in Ca concentration was very large: the highest Ca concentrations were found in old leaves (20–39 mg·g⁻¹), those in young leaves were much lower (14–20 mg·g⁻¹), and the lowest Ca concentrations were found in the fruits, 0.6–1.4 mg·g⁻¹ (Tables 3, 4, and 5). The Ca concentration in the fruits decreased as they developed and ripened (Tables 3, 4, and 5).

The calcium concentrations in plant organs, especially the leaves and roots, increased as the solution N-NO₃:N-NH₄ ratio increased (Tables 4 and 5) and similar results were obtained in the earlier plant and leaf samples (data not shown). No significant effect of the solution N-NO₃:N-NH₄ ratio on Ca concentration in the fruits was observed in the aero-hydroponics system (Expt. 2), whereas in the tuff medium (Expt. 3), the Ca concentration in the fruits increased significantly as this ratio increased (Table 5). In the tuff medium, where the Ca concentration distribution in fruit was determined, it was three times higher in the distal part than the blossom end, in agreement with published data (Marcelis and Ho, 1999), and the effect of the N-NO₃:N-NH₄ ratio on Ca concentration was significant in each part (Table 5).

Ca concentrations in plant organs (leaf, root, fruit) at the end of Expt. 1 decreased as N concentration in the solution increased above 3.5 mmol·L⁻¹ (Table 3) and similar results were obtained in fruit and leaf samples throughout the experiment (data not shown). This effect is probably due to the increased NH₄ concentration and consequently reduced Ca uptake as the N concentration increased.

The potassium concentration was of the same order in young and old leaves and the fruits (Tables 3, 4 and 5). Thus the K:Ca ratio in the fruit was in the range of 40:1 to 50:1, whereas in the old leaves it ranged from 1:1 to 3:1. Like that of Ca, the K concentration in all organs decreased as the solution N-NO₃:N-NH₄ ratio decreased (Tables 4 and 5), because of the anion-cation balance mechanism in the plant (Kirkby and Mengel, 1967). The effect of the solution N concentration at constant N-NO₃:N-NH₄ ratio on the K concentrations in plant organs was less clear: there was a K concentration maximum in the leaves in the N concentration range of 7.0 to 10.5 mmol·L⁻¹, whereas the K concentration in the fruits decreased as the N supply increased, in the range studied.

The Mg distribution in plant organs was similar to that of K. The Mg concentration in the fruits was lower than that in the leaves,

Table 5. Mineral composition in leaves and Ca concentration in fruits as affected by N-NO₃:N-NH₄ ratio in the nutrient solution in Expt. 3.

One. Old and young leaves								
NO ₃ /NH ₄	Ca	Mg	K	N	Ca	Mg	K	N
molar ratio	mg·g ⁻¹				mg·g ⁻¹			
	Old leaves				Young leaves			
1	38.0	10.9	68.0	53.0	8.7	3.0	27.0	83.0
3	40.4	11.4	71.0	47.0	9.9	3.4	30.0	79.0
9	45.6	12.0	73.0	44.0	12.4	4.0	34.0	76.0
LSD _{0.05}	1.4	0.4	2.3	6.0	1.4	0.4	5.0	6.0
F prob.	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Two. Flowers and fruitlets								
NO ₃ /NH ₄	Ca	Mg	K	N	Ca	Mg	K	N
molar ratio	mg·g ⁻¹				mg·g ⁻¹			
	Flowers				Fruitlets			
1	12.6	3.47	29.4	48.1	1.75	2.6	27.2	61.7
3	13.7	3.86	31.3	47.7	2.28	2.6	30.0	60.0
9	14.5	4.10	31.2	45.9	2.44	2.7	34.7	59.5
LSD _{0.05}	0.4	0.08	0.4	0.7	0.16	0.02	0.7	0.9
F prob.	0.018	<0.0001	0.0052	0.078	0.046	0.011	0.001	NS
Three. Fruits at different developmental stages and divided into three sections.								
NO ₃ /NH ₄	Ca	Mg	K	N				
molar ratio	mg·g ⁻¹							
	Average ages and sections							
1.0	0.79	1.83	30.1	48.0				
3.0	0.83	1.87	30.6	45.7				
9.0	1.00	2.16	35.1	43.5				
LSD _{0.05}	0.026	0.035	0.8	0.6				
Location	Average ages and NO ₃ /NH ₄ treatments							
Dorsal	1.52	2.00	27.6	48.7				
Median	0.59	1.79	30.5	42.7				
Blossom end	0.51	2.06	37.7	45.7				
LSD _{0.05}	0.03	0.03	1.1	0.6				
Stage	Average sections and NO ₃ /NH ₄ treatments							
Young	0.96	2.15	31.9	50.2				
Green	1.02	2.08	33.3	47.1				
Half red	0.78	1.91	35.4	46.1				
Red	0.73	1.67	29.0	39.5				
LSD _{0.05}	0.03	0.04	0.9	0.7				
Analysis of variance (F probability)								
NO ₃ /NH ₄	<0.0001	<0.0001	<0.0001	<0.0001				
Stage	<0.0001	<0.0001	0.002	<0.0001				
Location	<0.0001	<0.0001	<0.0001	<0.0001				
NO ₃ /NH ₄ × Stage	NS	NS	NS	0.0505				
NO ₃ /NH ₄ × Location	0.037	NS	0.017	NS				
Stage × Location	0.0001	NS	0.13	NS				

^{NS}Nonsignificant.

but the Mg:Ca ratio in the fruits was higher than 2:1, whereas in the old leaves it was lower than 0.5:1.0 (Tables 3, 4, and 5). As the solution N-NO₃:N-NH₄ ratio increased, the Mg concentrations increased considerably and significantly in old leaves, roots and fruits (Tables 4 and 5). As the total N concentration increased, the Mg concentration decreased in all organs except the stem, probably as a result of dilution (in the range of 0.25–7.0 mmol·L⁻¹) and charge balance (in the range of 7.0–14.0 mmol·L⁻¹).

Discussion

Fruit yield and quality. The effects of the NH₄ concentration on total and high-quality fruit yields were investigated in the present study in two ways: changing the NH₄ concentration at a constant N-NO₃:N-NH₄ ratio of 4:1 and changing the NH₄ concentration at a constant total N (NO₃+NH₄) concentration of 7.0 mmol·L⁻¹. By combining the data obtained in these two ways, we observed that

total fruit yield decreased linearly as the NH₄ concentration increased above 1.0 mmol·L⁻¹ in Expts. 1 and 2 and above 2.0 mmol·L⁻¹ in Expt. 3 (Fig. 3). In the three experiments a sharp decline in high-quality yield was obtained as the NH₄ concentration increase above 2.0 mmol·L⁻¹. Thus, the negative effects on total and high-quality yields of increasing the N concentration above 7 mmol·L⁻¹, may be attributed to the change in NH₄ concentration. The fruit yield increased threefold as the NH₄ concentration increased from 0.05 to 1.0 mmol·L⁻¹ (Expt. 1, Fig. 3), however in this range of NH₄ concentrations the N concentration was probably the limiting factor for yield.

The effects of both the solution N concentration and the N-NH₄:N-NO₃ ratio on the incidence of BER may be attributed to changes in NH₄ concentration (Fig. 4): the incidence of BER increased as the NH₄ concentration increased from 1.5 to 3.5 mmol·L⁻¹. The effect of NH₄ on BER observed in the present study is consistent with those reported previously for tomato (Ho et al. 1993; Wilcox et al.

Fig. 4. Effect of NH_4 concentration in the solution on: (a) The incidence of BER ($\square$) (Expts. 1 and 2, 30 Apr. 1996); (b) The incidence of flat fruits ($\circ$) (Expts. 1 and 2, 30 Apr. 1996); and (c) the incidence of BER ($\blacksquare$) and the fruit length-to-diameter ratio ($\bullet$) (Expt. 3, 8 June 1997). The empty symbols are for Expt. 1 (N varied from 0.25 to 14.00 mmol L⁻¹) and the full symbols are for Expt 2 and Expt 3 (constant N, 7.0 mmol L⁻¹). The lines for BER and flat fruit in Figs. (a) and (b) are the best fitted polynomial and linear regressions, respectively. The lines in (c) were drawn through the data points. Error bars are SE.

1973; Wojciechowski et al. 1969) and pepper (Marti and Mills, 1991).

The increase in the incidence of flat fruits (or the reduction in length to circumference ratio) with increasing NH_4 concentration was linear over the range studied, independently of the means of increasing the NH_4 concentration (Fig. 4). The effect of the $\text{N-NO}_3^-:\text{N-NH}_4^+$ ratio on the development of flat fruit has not been reported previously. This phenomenon may be related to the sink : source balance and the development of flower organs. Ganmore-Newmann and Kafkafi (1983) reported that a high NH_4 fraction in the solution N resulted in

deformation of the strawberry pollen grain. Aloni et al. (1999) showed that the production of flat pepper fruits was enhanced by the removal of fruits, which form a strong sink, from the plant. Monitoring the development of the new flowers after the fruit removal showed that the ovaries of these flowers were much bigger than normal and, consequently, deformed fruits were produced (Aloni et al., 1999). High NH_4 concentrations did not affect leaf weights but decreased the stem dry matter production (Bar-Tal et al., 2001), another strong sink for carbohydrates. However, it is not yet clear whether or not these changes are related

to the deformation of the flowers and consequently fruits.

Mineral composition of plant organs. The large decrease in reduced-N concentration in the pepper organs as the $\text{N-NO}_3^-:\text{N-NH}_4^+$ ratio increased, observed in the present study, is also unique, as no such effect has been reported previously, for tomato (Feigin et al. 1980; Ganmore-Newmann and Kafkafi, 1980b), rose (Feigin et al. 1984) and pepper (Marti and Mills, 1991). The pattern of decrease in N content as a function of the $\text{N-NO}_3^-:\text{N-NH}_4^+$ ratio is consistent with our nitrogen uptake data (Bar-Tal et al., 2001). As the $\text{N-NO}_3^-:\text{N-NH}_4^+$ ratio increased from 0.25:1 to 2:1, the total N uptake was not affected, but the dry matter production increased, causing the N concentration in the plant organs to decrease because of the dilution effect, since N uptake is controlled by dry weight, according to allometric relationships (Cardenas-Navarro et al., 1998). A further increase in the $\text{N-NO}_3^-:\text{N-NH}_4^+$ ratio reduced N uptake [in agreement with reported findings on the kinetics of NO_3^- and NH_4^+ uptakes (Reid, 1999)] with no effect on DM production, so that there was a further decrease in N concentration in the plant organs.

The pattern of Ca distribution in pepper organs can be explained by the following concept: Ca transport in the plant is dominated by transport via the xylem (Hanson, 1984), therefore, new developing organs (such as young leaves and fruits) contain low Ca concentrations (Ho, 1989; Ho et al., 1993; Wiersum, 1966). The distribution of K and Mg in plant organs observed in the present study is consistent with published data on tomato (Bar-Tal et al., 1994, 1996; Ganmore-Newmann and Kafkafi, 1980b; Kirkby and Mengel, 1967) and pepper (Marti and Mills, 1991). The NH_4^+ supply reduced K, Mg, and Ca concentrations in plant organs, through the mechanism of charge balance in ion uptake, since nitrogen is a dominant macro-nutrient, its ionic form controls cation and anion uptake as was also reported elsewhere for tomato (Kirkby and Mengel, 1967; Ganmore-Newmann and Kafkafi, 1980b). The effect of the N form on Ca concentrations in plant organs, especially the fruit, was larger in the tuff system than in the aero-hydroponics, probably because of the difference in pH. In the aero-hydroponics system the pH was kept almost constant, whereas in the tuff system the pH of the drained solution of the highest NH_4 treatment, decreased to a minimum of 5.0, one unit lower than that in the low NH_4 treatment (6.0). Low pH reduces the uptake of Ca and other cations, in accordance with the key role of the plasma membrane-bound proton efflux pump as the driving force for ion uptake (Marschner, 1995).

BER correlation with Ca concentration. Although the Ca supply to the fruit is considered to be an important factor in the occurrence of BER, efforts to define critical values or even to correlate BER incidence with Ca concentration or K/Ca ratio in tomato fruits have failed in many experiments (Chiu and Bould, 1976; Nonami et al., 1995). Possible reasons are either: 1) the fruit is susceptible to the Ca concentration and the K/Ca ratio only

Fig. 5. Correlation of blossom end rot occurrence with Ca concentration in (a) young fruits (■) (Expts. 1 and 2) and (b) the dorsal part (●) and the blossom end (▲) of young fruits (Expt. 3).

during a very short period in early fruit development (Ehret and Ho, 1986; Ho, 1989; Ho et al., 1993; Marti and Mills, 1991; Marcelis and Ho, 1999); or 2) the Ca concentration in the fruit is very low and varies with the distance between the distal part and the blossom end (Ehret and Ho, 1986; Ho et al., 1987; Marcelis and Ho, 1999). In the current study, BER incidence was well correlated with Ca content in young fruits (Fig. 5). The specific stage of fruit development is crucial, since Ca concentration in the fruit decreased during fruit growth and ripening. Better correlation of the BER incidence with Ca concentration was obtained in Experiment 3, when analyses of fruit sections were used (Fig. 3). The critical Ca concentration for the induction of BER may vary with environmental conditions that affect fruit growth rate (Ho et al., 1993; Marcelis and Ho, 1999).

Conclusions

The optimal N concentration for maximum high-quality yield was 8.2 mmol L^{-1} . Increasing the NH_4 concentration in the solution enhanced the incidence of BER and the development of flat fruits. Therefore, the high-quality yield increased as the $\text{N-NO}_3^- : \text{N-NH}_4^+$ ratio increased (up to 4:1 and 9:1 in the aero-hydroponics and growth medium experiments, respectively), although this ratio had no significant effect on leaf weight and area (Bar-Tal et al., 2001). When the $\text{N-NO}_3^- : \text{N-NH}_4^+$ ratio of 4:1 was kept constant, increasing the NH_4 concentration above

1.0 mmol L^{-1} reduced fruit quality. The incidence of BER was well correlated with the Ca contents in tissues of young fruits and at specific locations in the organ.

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