Nitrogen Nutrition of Greenhouse Pepper. I. Effects of Nitrogen Concentration and NO$_3$ : 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 N-NO$_3$ : 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 mmol·L$^{-1}$, with a constant N-NO$_3$ : N-NH$_4$ ratio of 4); Expt. 2 included five treatments of different N$^-$ NO$_3$ : NH$_4$ molar ratios (0.25 to 4, with a constant N concentration of 7 mmol·L$^{-1}$); and Expt. 3 included three treatments of different N$^-$ NO$_3$ : NH$_4$ molar ratios (1.0, 3.0, and 9.0, with a constant N concentration of 7 mmol·L$^{-1}$). Plants were grown in an aeroponics 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 mmol·L$^{-1}$, respectively. The total and high-quality fruit yields both increased with increasing N-NO$_3$ : 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 mmol·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spring and summer, because of blossom-end rot (BER) and shape deformation of fruits (Israel Ministry of Agriculture, unpublished data).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 N-NO$_3$ : 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 (Gannmore-Neumann and Kafkafi, 1980a). Feigin et al. (1984), consisting of two separate 50 × 29 × 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 mmol·L$^{-1}$ (with constant N-NO$_3$ : N-NH$_4$ ratio of 4:1) and Expt. 2 included five N-NO$_3$ : NH$_4$ ratios, 0.25, 0.50, 1.00, 2.00, and 4.00 (at a constant N concentration of 7 mmol·L$^{-1}$) (Table 1). The treatment with N-NO$_3$ : 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 mmol·L$^{-1}$) 0.2 NO$_3$, 4 Cl, 1.5 SO$_4$, 0.1 HCO$_3$, 2 Ca, 3 Mg, and 3 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 dS·m$^{-1}$.
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. In Expts. 1 and 2 the solutions contained 1.0 mmol·L⁻¹ (NH₄)₂SO₄, 0.25 mmol·L⁻¹ H₃BO₄, 1.0 mmol·L⁻¹ H₂PO₄, and 0.25 mmol·L⁻¹ MgSO₄. In Expt. 3 the solutions contained 1.0 mmol·L⁻¹ Mg(NO₃)₂.

Pepper seedlings were grown in a commercial nursery until four true leaves developed, in speedlings 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 as 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).

**Table 1. Composition of the nutrient solution in the three experiments.**

<table>
<thead>
<tr>
<th>N</th>
<th>NO₃</th>
<th>NH₄</th>
<th>NH₄NO₃</th>
<th>HNO₃</th>
<th>KNO₃</th>
<th>KCl</th>
<th>Mg(NO₃)₂</th>
<th>MgSO₄</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.25</td>
<td>0.20</td>
<td>0.05</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>5.0</td>
<td>0.0</td>
<td>1.0</td>
</tr>
<tr>
<td>3.5</td>
<td>2.80</td>
<td>0.70</td>
<td>0.7</td>
<td>0.0</td>
<td>2.1</td>
<td>2.9</td>
<td>0.0</td>
<td>1.0</td>
</tr>
<tr>
<td>7.0</td>
<td>5.60</td>
<td>1.40</td>
<td>1.4</td>
<td>0.0</td>
<td>4.2</td>
<td>0.8</td>
<td>0.0</td>
<td>1.0</td>
</tr>
<tr>
<td>10.5</td>
<td>8.40</td>
<td>2.10</td>
<td>2.1</td>
<td>1.3</td>
<td>5.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>14.0</td>
<td>11.20</td>
<td>2.80</td>
<td>2.8</td>
<td>1.3</td>
<td>5.0</td>
<td>0.0</td>
<td>1.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

**Expt. 1. Increasing N at a constant N-NH₄ : N-NO₃ ratio of 4.0.**

<table>
<thead>
<tr>
<th>N</th>
<th>NO₃</th>
<th>NH₄</th>
<th>NH₄NO₃</th>
<th>HNO₃</th>
<th>KNO₃</th>
<th>KCl</th>
<th>Mg(NO₃)₂</th>
<th>MgSO₄</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.25</td>
<td>1.40</td>
<td>5.60</td>
<td>1.4</td>
<td>0.0</td>
<td>0.0</td>
<td>2.1</td>
<td>5.0</td>
<td></td>
</tr>
<tr>
<td>0.50</td>
<td>2.33</td>
<td>4.66</td>
<td>0.0</td>
<td>0.0</td>
<td>1.15</td>
<td>5.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.00</td>
<td>3.50</td>
<td>3.50</td>
<td>3.5</td>
<td>0.0</td>
<td>5.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.00</td>
<td>4.66</td>
<td>2.33</td>
<td>2.3</td>
<td>2.3</td>
<td>0.0</td>
<td>2.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4.00</td>
<td>5.60</td>
<td>1.40</td>
<td>1.4</td>
<td>4.2</td>
<td>0.0</td>
<td>0.8</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Expt. 2. Increasing N-NH₄ : N-NO₃ ratio at a constant total N concentration of 7.0 mmol·L⁻¹.**

<table>
<thead>
<tr>
<th>N-NH₄</th>
<th>NO₃</th>
<th>NH₄</th>
<th>NH₄NO₃</th>
<th>HNO₃</th>
<th>KNO₃</th>
<th>KCl</th>
<th>Mg(NO₃)₂</th>
<th>MgSO₄</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.25</td>
<td>1.50</td>
<td>3.50</td>
<td>3.5</td>
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<td>0.0</td>
<td>5.0</td>
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</tr>
<tr>
<td>1.00</td>
<td>4.66</td>
<td>2.33</td>
<td>2.3</td>
<td>2.3</td>
<td>0.0</td>
<td>2.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.00</td>
<td>6.30</td>
<td>0.70</td>
<td>0.7</td>
<td>0.7</td>
<td>0.6</td>
<td>5.0</td>
<td>0.0</td>
<td></td>
</tr>
</tbody>
</table>

**Expt. 3. Increasing N-NH₄ : N-NO₃ ratio at a constant total N concentration of 7.0 mmol·L⁻¹.**

In the three experiments, all solutions contained 1.0 mmol·L⁻¹ H₂PO₄, 27.9 µmol·L⁻¹ Fe as Sequestrin, 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 H₃BO₄.

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

<table>
<thead>
<tr>
<th>NO₃/NH₄</th>
<th>Total Yield</th>
<th>High quality yield</th>
<th>BER</th>
<th>Length : diameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>144.8 a</td>
<td>67.1 a</td>
<td>22.7 a</td>
<td>0.959 a</td>
</tr>
<tr>
<td>3</td>
<td>148.2 a</td>
<td>63.2 b</td>
<td>27.3 b</td>
<td>0.941 b</td>
</tr>
<tr>
<td>9</td>
<td>130.4 a</td>
<td>67.1 a</td>
<td>22.7 a</td>
<td>0.959 a</td>
</tr>
<tr>
<td>1.5</td>
<td>1.67</td>
<td>1.69</td>
<td>1.26</td>
<td>0.0047</td>
</tr>
</tbody>
</table>

Fig. 1. Total (■) and high-quality (▲) fruit yields as a function of total N concentration (N-NH₄ : N-NO₃ ratio of 4.0, Expt. 1, 30 Apr. 1996) and as a function of N-NH₄ : N-NO₃ 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.
Fruit number, weight, and physiological determination of the experiment, 287 DAT. Fruits were harvested from 99 DAT to the removed frequently as in Expts. 1 and 2. Red two main plant stems; lateral branches were supported Vertical threads and plastic rings supported irrigation and drainage water was in the range density on the ground was 3.3 plants/m². Six row centers was 1.8 m, and plant ure) contained tuff medium; the distance containers per row. Each container (50 cm width, randomized blocks, each plot included six constraints of differing N-NO₃ : N-NH₄ ratios: 1.0, 2.5, 3.0 and 9.0 (all with N concentration of 7.0 mmol·L⁻¹). In order to obtain 1 mmol P and 5 mmol 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 mmol NO₃, 4 mmol Cl, 2 mmol H₂CO₃, 1.5 mmol SO₄, 1.5 mmol Ca, 1 mmol Mg, and 3.5 mmol 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-
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 NH₄ 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 NO₃ : NH₄ ratio (N = 7 mmol L⁻¹) in the nutrient solution.

<table>
<thead>
<tr>
<th>NO₃/NH₄ molar ratio</th>
<th>Ca</th>
<th>Mg</th>
<th>K</th>
<th>N</th>
<th>Ca</th>
<th>Mg</th>
<th>K</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.25</td>
<td>5.1</td>
<td>5.5</td>
<td>21.9</td>
<td>35.3</td>
<td>4.0</td>
<td>2.3</td>
<td>14.8</td>
<td>57.3</td>
</tr>
<tr>
<td>0.50</td>
<td>5.0</td>
<td>5.2</td>
<td>22.2</td>
<td>34.4</td>
<td>4.6</td>
<td>2.4</td>
<td>14.6</td>
<td>62.4</td>
</tr>
<tr>
<td>1.00</td>
<td>5.3</td>
<td>4.9</td>
<td>25.9</td>
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<td>4.7</td>
<td>2.3</td>
<td>14.0</td>
<td>63.0</td>
</tr>
<tr>
<td>2.00</td>
<td>5.3</td>
<td>4.5</td>
<td>26.5</td>
<td>27.4</td>
<td>6.3</td>
<td>3.0</td>
<td>26.1</td>
<td>67.2</td>
</tr>
<tr>
<td>4.00</td>
<td>5.5</td>
<td>4.3</td>
<td>25.4</td>
<td>23.3</td>
<td>6.7</td>
<td>3.0</td>
<td>25.9</td>
<td>64.8</td>
</tr>
<tr>
<td>LSDₜₐₜ</td>
<td>0.17</td>
<td>0.28</td>
<td>0.9</td>
<td>0.8</td>
<td>0.3</td>
<td>0.1</td>
<td>1.8</td>
<td>3.8</td>
</tr>
<tr>
<td>F prob.</td>
<td>ns</td>
<td>0.046</td>
<td>0.010</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>0.0005</td>
<td>&lt;0.0001</td>
<td>ns</td>
</tr>
<tr>
<td>Old leaves</td>
<td>ns</td>
<td>0.0032</td>
<td>0.039</td>
<td>ns</td>
<td>0.039</td>
<td>ns</td>
<td>0.005</td>
<td></td>
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</tbody>
</table>

Fruits at different developmental stages

<table>
<thead>
<tr>
<th>NO₃/NH₄ molar ratio</th>
<th>Ca</th>
<th>Mg</th>
<th>K</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.25</td>
<td>23.8</td>
<td>11.5</td>
<td>61.8</td>
<td>50.3</td>
</tr>
<tr>
<td>0.50</td>
<td>25.8</td>
<td>12.6</td>
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<td>49.0</td>
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<td>20.5</td>
<td>9.8</td>
<td>69.3</td>
<td>45.3</td>
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<td>2.00</td>
<td>29.7</td>
<td>14.5</td>
<td>68.6</td>
<td>44.4</td>
</tr>
<tr>
<td>4.00</td>
<td>30.3</td>
<td>15.6</td>
<td>76.0</td>
<td>45.8</td>
</tr>
<tr>
<td>LSDₜₐₜ</td>
<td>0.8</td>
<td>0.4</td>
<td>2.3</td>
<td>2.2</td>
</tr>
<tr>
<td>F prob.</td>
<td>0.0001</td>
<td>0.0002</td>
<td>0.039</td>
<td>ns</td>
</tr>
</tbody>
</table>

Analysis of variance (F probability)

<table>
<thead>
<tr>
<th>NO₃/NH₄ × stage</th>
<th>NS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Block</td>
<td>NS</td>
</tr>
<tr>
<td>NO₃/NH₄ × stage</td>
<td>NS</td>
</tr>
</tbody>
</table>

Results

1. 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 mmol L⁻¹ resulted in increases of high-quality yield and total yield by 350% and 550%, respectively. A further increase of the solution N concentration from 7 to 14 mmol L⁻¹ reduced the high-quality yield by 32%. The calculated N concentration for maximum yield was 9.4 mmol 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 mmol L⁻¹, probably because of the effect of NH₄ on the incidence of BER and flat fruit.

The solution N-NO₃ : N-NH₄ 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-NO₃ : N-NH₄ 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 steeper than that for total yields (Fig. 1a). The increase in total yield with the increasing N-NO₃ : N-NH₄ ratio resulted mainly from the reduction of fruit physiological disorders, which reduced fruit mean weight. Extending the maximal N-NO₃ : N-NH₄ 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 mmol L⁻¹ had no effect on the incidence of BER, but as the N concentration increased from 7.0 to 10.5 mmol L⁻¹ the incidence of BER increased significantly and a further increase to 14 mmol L⁻¹ had no effect (Fig. 2). This pattern was best described by a polynomial curve of the third order.

The N-NO₃ : N-NH₄ 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-NO₃ : N-NH₄ 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 mmol L⁻¹ (Expt. 1, Fig. 2).

The N-NO₃ : N-NH₄ 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).

The solution 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), 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 magnesium 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, when 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 of the nutrient solution in Expt. 1 decreased as N concentration in the solution increased above 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, 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 increased 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-NO₃:N-NH₄ 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.)
Neumann and Kafkafi (1983) reported that a development of flower organs. 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 N-NO₃ : N-NH₄ ratio is consistent with our nitrogen uptake data (Bar-Tal et al., 2001). As the N-NO₃ : N-NH₄ 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 N-NO₃ : N-NH₄ ratio reduced N uptake [in agreement with reported findings on the kinetics of NO₃ and NH₄ 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 NH₄ 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 NH₄ treatment, decreased to a minimum of 5.0, one unit lower than that in the low NH₄ 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).

**Fig. 4.** Effect of NH₄ concentration in the solution on: (a) The incidence of BER (Q) (Expts. 1 and 2, 30 Apr. 1996); (b) The incidence of flat fruits (O) (Expts. 1 and 2, 30 Apr. 1996); and (c) the incidence of BER (■) and the fruit length-to-diameter ratio (●) (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.

The increase in the incidence of flat fruits (or the reduction in length to circumference ratio) with increasing NH₄ concentration was linear over the range studied, independently of the means of increasing the NH₄ concentration (Fig. 4). The effect of the N-NO₃ : N-NH₄ 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 NH₄ 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 NH₄ 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 N-NO₃ : N-NH₄ 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 decrease in N content as a function of the N-NO₃ : N-NH₄ 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 N-NO₃ : N-NH₄ ratio reduced N uptake [in agreement with reported findings on the kinetics of NO₃ and NH₄ uptakes (Reid, 1999)] with no effect on DM production, so that there was a further decrease in N concentration in the plant organs.

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
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 N-NO\(_3\) : N-NH\(_4\) ratio increased (up to 4:1 and 9:1 in N-NO\(_3\) : 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.

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 N-NO\(_3\) : 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 N-NO\(_3\) : 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.

Literature Cited


