HORTSCIENCE 36(7):1252–1259. 2001.

Nitrogen Nutrition of Greenhouse Pepper. II. Effects of Nitrogen Concentration and $NO_3 : NH_4$ Ratio on Growth, Transpiration, and Nutrient Uptake

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Additional index words. nitrogen, calcium, potassium, *Capsicum annuum*

Abstract. **The objective of this research was to study the effects of N concentration and $N\text{-}NO_3 : N\text{-}NH_4$ ratio in the nutrient solution on growth, transpiration, and nutrient uptake of greenhouse-grown pepper in a Mediterranean climate. The experiment included five total N levels (0.25 to 14 $mmol·L^{–1}$, with a constant $N\text{-}NO_3 : N\text{-}NH_4$ ratio of 4) and five treatments of different $N\text{-}NO_3 : N\text{-}NH_4$ ratios (0.25 to 4, with a constant N concentration of 7 $mmol·L^{–1}$). Plants were grown in an aero-hydroponic system in a climate-controlled greenhouse. The optimum N concentrations for maximum stem and leaf dry matter (DM) production were in the range of 8.0 to 9.2 $mmol·L^{–1}$. The optimum $N\text{-}NO_3 : N\text{-}NH_4$ ratio for maximal stem DM production was 3.5. The optimum value of N concentration for total fruit DM production was 9.4 $mmol·L^{–1}$. Fruit DM production increased linearly with increasing $N\text{-}NO_3 : N\text{-}NH_4$ ratio in the range studied. The N concentration, but not N source, affected leaf chlorophyll content. Shorter plants with more compacted canopies were obtained as the $N\text{-}NO_3 : N\text{-}NH_4$ ratio decreased. The effect of N concentration on transpiration was related to its effect on leaf weight and area, whereas the effect of a decreasing $N\text{-}NO_3 : N\text{-}NH_4$ ratio in reducing transpiration probably resulted from the compacted canopy. Nitrogen uptake increased as the N concentration in the solution increased. Decreasing the $N\text{-}NO_3 : N\text{-}NH_4$ ratio increased the N uptake, but sharply decreased the uptake of cations, especially Ca.**

Greenhouse grown bell pepper (*Capsicum annuum* L.) is a relatively new crop with a high economic potential in Israel. Continuous high yield production of high-quality fruits is required for economic success of the industry. However, the fruit yields obtained in greenhouses are lower than those obtained in Europe, and the fruit quality deteriorates from the spring onwards in experimental and commercial greenhouses (Israel Ministry of Agriculture, unpublished data).

A lot of information on N requirement by bell pepper has been obtained from open-field experiments involving appropriate cultivars. In the majority of the experiments N application increased the number of flowers and the fruit yield (Maynard et al., 1969). The optimal N application varied from 135 to 252 $kg·ha^{–1}$, depending on environmental conditions and soil fertility (Hartz et al., 1993; Locascio and Stall, 1994). Sagiv et al. (1987) demonstrated the importance of the application rate in relation to crop demand. They established the N consumption curve of field-grown pepper (cv. Maor) in Israel. Higher yields were obtained with continuous fertigation applied with drippers and adjusted to the consumption curve, than with split application of N via sprinkler irrigation. Aloni et al. (1994) found that the optimal N concentration in the irrigation water for traditional open-field cultivars varied between 7 and 17.5 $mmol·L^{–1}$, depending on irradiation and cultivar. Schon et al. (1994) found that plants grown in rockwool medium receiving N at 12.5 $mmol·L^{–1}$ produced significantly more fruit and higher total fruit weight than plants receiving N at 8.6 $mmol·L^{–1}$. The difference in cultivars, cultural practices and micro-climate between field and greenhouse grown bell pepper lead to different growth curves and yields, and consequently, water and nutrient consumption (Tzipilevitz et al. 1996). Recently, Qawasmi et al. (1999) found that maximum yield of greenhouse grown bell pepper was obtained at 150 $Kg·ha^{–1}$ N rate, and the maximum growth rate and accumulation of dry matter in the fruits occurred 90 to 150 d after planting. There is a lack of information on the optimal N consumption curves of the new greenhouse-grown pepper cultivars under a Mediterranean climate.

Nitrogen form is an important factor for plant development and yield. High $N\text{-}NO_3 : N\text{-}NH_4$ ratio in the fertilizer damaged sugar beets (*Beta vulgaris* L.) through acidification of the rhizosphere (Breteler, 1973). However, buffering the solution pH improved plant tolerance to a high $N\text{-}NO_3 : N\text{-}NH_4$ ratio (Arnon et al., 1942). Increasing the $N\text{-}NH_4 : N\text{-}NO_3$ ratio in the N fertilizer reduced the uptake of other mineral cations, but increased the uptake of mineral anions in tomato (Kirkby and Mengel, 1967; Ganmore-Neumann and Kafkafi, 1980b) and pepper (Marti and Mills, 1991a, 1991b), while Sarro et al. (1995) reported that ammonium reduced Ca and Mg uptake by pepper, but had no effect on K uptake.

A $N\text{-}NO_3 : N\text{-}NH_4$ ratio of 1:1 has been found to be the optimal for tomato plants, under wide range of root temperatures (Ganmore-Neumann and Kafkafi, 1980a). Marti and Mills (1991a) reported that in bell pepper $N\text{-}NH_4$ reduced dry weight and fruit yield relative to $N\text{-}NO_3$ in the fertilizer. In the Netherlands the recommended $N\text{-}NO_3 : N\text{-}NH_4$ ratio for greenhouse pepper is ≈6:1 (Roorda van Eysinga and van der Meijs, 1981), whereas in later recommendations the ratio increased to 12:1 (Leo Marcelis, personal communication). However, in semi-arid regions, NH_4 is used as a mean to reduce the pH of the medium for preventing salts precipitation. Sarro et al. (1995) reported that replacing the N source from just $N\text{-}NO_3$ to $NO_3 : NH_4$ ratio of 6:1 (2.0 $mmol·L^{–1}$ NH_4) had no significant effect on fruit yield of greenhouse grown pepper. Zornoza et al. (1989) reported increased sensitivity of bell pepper to NH_4 under high radiation. Takacs and Tecsi (1992) found that a low $N\text{-}NO_3 : N\text{-}NH_4$ ratio in the nutrient solution caused destruction of leaf chloroplasts. The optimal $NO_3 : NH_4$ ratio for greenhouse-grown pepper in Mediterranean climate has yet to be determined.

The objective of our research was to investigate the effects of N concentration and $NO_3 : NH_4$ ratio on plant growth, dry matter production, uptake of nutrients, and transpiration of greenhouse-grown pepper.

Materials and Methods

Plant growth and experimental design. The two experiments, 1 and 2, have been described in detail by Bar-Tal et al. (2001). Briefly, 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 × 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 140-L container and recirculated. Expt. 1 included

Received for publication 9 May 2000. Accepted for publication 9 Apr. 2001. Contribution no. 603/99, 1999 series, from the Agricultural Research Organization, The Volcani Center, Bet-Dagan, Israel. We thank Beni Bar-Yosef and Avner Silber for their beneficial suggestions in improving the manuscript. This research has been financed by the Israeli chief scientist of the Ministry of Agriculture, project no. 301-0234-95.
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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 : N-NH_4 ratios, 0.25, 0.5, 1, 2, and 4 (at a constant N concentration of 7.0 mmol·L^{-1}) (Table 1). The treatment with N-NO_3 : N-NH_4 ratio of 4 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, 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 2.0–2.5 dS·m^{-1} (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, both the input and output of water were determined by a water gauge. In that period of time the concentration of NH_4 declined much faster than that of NO_3, therefore, the concentrations of NH_4 and NO_3, were determined weekly; $(NH_4)_2SO_4$ and HNO_3 in the proper ratio were added weekly to adjust the N-NO_3 : N-NH_4 ratio and the total N concentration. The mineral compositions (NH_4, NO_3, K, Ca, and Mg) of the input and output solutions were analyzed, and the transpiration and nutrient uptake were determined from the changes in the solution volume and concentrations.

Pepper seedlings were grown in a commercial nursery until four true leaves developed, in speedlings trays (pyramid cells of 19.36 cm^2 area, 15 cm^3 volume), in a 1 peat : 1 vermiculite mixture (v/v). Twelve uniform seedlings with 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/m^2, 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-NO_3 : N-NH_4 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. 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 yield was determined.

At the end of the experiment the plants from each container were pooled together and divided into root, stem, leaves, and fruits for determination dry matter weight (DM) of the organs. Leaf area was determined by means of a flatbed scanner (HP IIcx; Hewlett Packard, Palo Alto, Calif.) for analysis with Delta-T Scan software (Delta-T Devices, Cambridge, U.K.).

Potassium concentration was determined

Table 1. The composition of the nutrient solutions used to grow plants at different total N concentration (Expt. 1) or different N-N O_3 : N-NH_4 ratios.[z]

Expt. 1. Increasing Nitrogen at a constant N-N O_3 : N-NH_4 ratio of 4.0.

N	NO_3	NH_4	NH_4NO_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_4NO_3	KNO_3	$(NH_4)_2SO_4$	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

[z]In the two experiments all solutions contained 1.0 mmol·L^{-1} H_3PO_4, 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 µmol·L^{-1} 0.7 Cu as EDTA chelates, and 40 µmol·L^{-1} H_3BO_4. In Expt. 2 the solutions contained 1.0 mmol·L^{-1} $MgSO_4$.

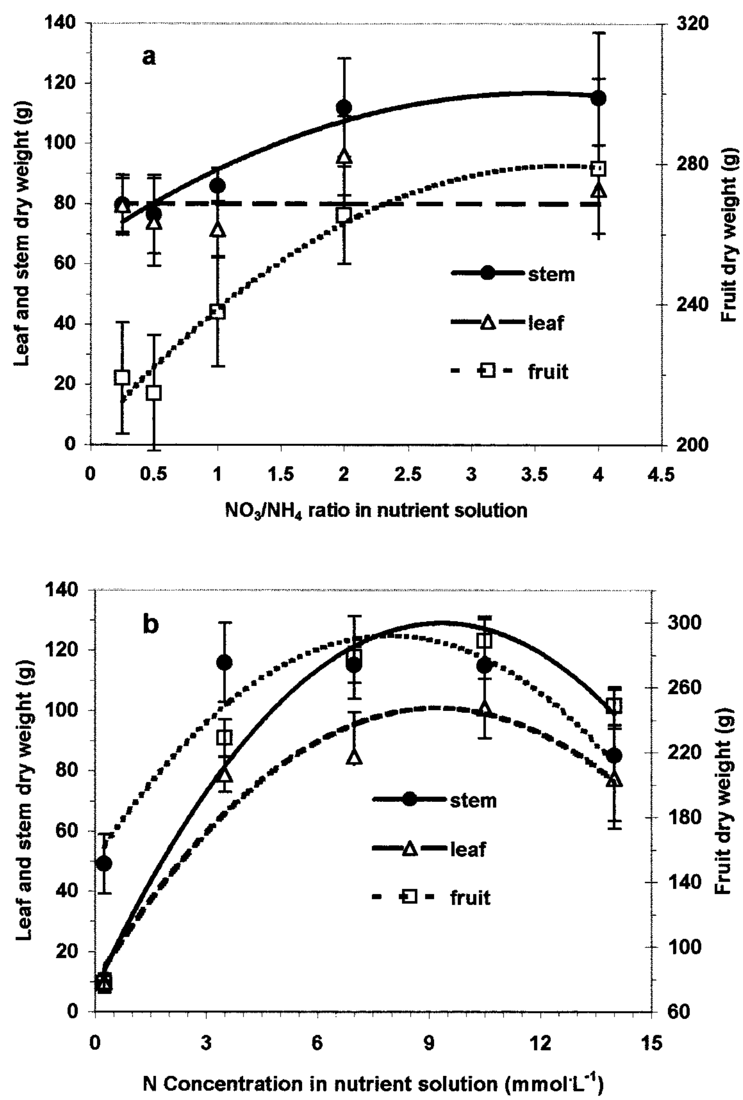

Fig. 1. Fruit, stem and leaf dry weights at the termination of the experiment (242 DAT) as a function of (**a**) N-NO_3 : N-NH_4 ratio (at a constant N concentration of 7.0 mmol·L^{-1}) and (**b**) total mineral N concentration (at a constant N-NO_3 : N-NH_4 ratio of 4.0). The equations of the lines and their parameters are presented in Table 2. Error bars present SE.

Table 2. Calculated coefficients of quadratic ($y = ax^2 + bx + c$) or linear ($y = ax + b$) relations between dry weight of pepper plant organs, stem length, shoot:root ratio, transpiration and nutrient uptake and

a. The solution $N\text{-}NO_3 : N\text{-}NH_4$ ratio (at a constant total N concentration of 7.0 $mmol{\cdot}L^{-1}$).

Variable	Figure	Equation	a	b	c	Maximum	R^2
						$NO_3 : NH_4$ ratio	
Fruit weight (g)	1 a	Quadratic	–5.5	41.2	202.7	3.7	0.97
Stem weight (g)	1 a	Quadratic	–4.0	28.1	67.0	3.5	0.93
Stem length (m)		Quadratic	– 0.2	1.2	2.0	3.0	0.82
Shoot : root ratio	2 a	Linear	0.4	6.4			0.57
Relative transpiration	4 a	Quadratic	1.7	–2.2	81.6	0.65[Z]	0.98
Relative N uptake	4 a	Quadratic	–1.8	3.8	114.0	1.1	0.68
Relative K uptake	4 c	Quadratic	–2.4	20.1	58.7	4.1	0.98
Relative Ca uptake	4 c	Quadratic	–1.3	13.8	65.9	5.3	0.89

b. The solution N concentration ($mmol{\cdot}L^{-1}$) (at a constant total $N\text{-}NO_3$:$N\text{-}NH_4$ ratio of 4.0).

Variable	Figure	Equation	a	b	c	Maximum	R^2
	Type					$mmol{\cdot}L^{-1}$	
Fruit weight (g)	1 b	Quadratic	–2.59	48.4	73.6	9.4	0.98
Stem weight (g)	1 b	Quadratic	–1.17	18.7	50.5	8.0	0.90
Leaf weight (g)	1 b	Quadratic	–1.07	19.7	9.8	9.2	0.94
Stem length (m)		Quadratic	-0.02	0.26	2.6	7.3	0.83
shoot:root ratio	2 b	Quadratic	–0.064	1.16	2.6	10.1	0.997
Relative transpiration[z]	4 b	Quadratic	–0.71	12.3	48.5	8.7	0.93
Relative N uptake	4 b	Quadratic	–0.80	20.1	12.5	12.5	0.96
Relative K uptake	4 d	Quadratic	–1.29	21.9	17.9	8.5	0.93
Relative Ca uptake	4 d	Quadratic	–1.07	15.1	53.5	7.0	0.95

[z]Minimum transpiration at this $N\text{-}NO_3 : N\text{-}NH_4$ ratio.

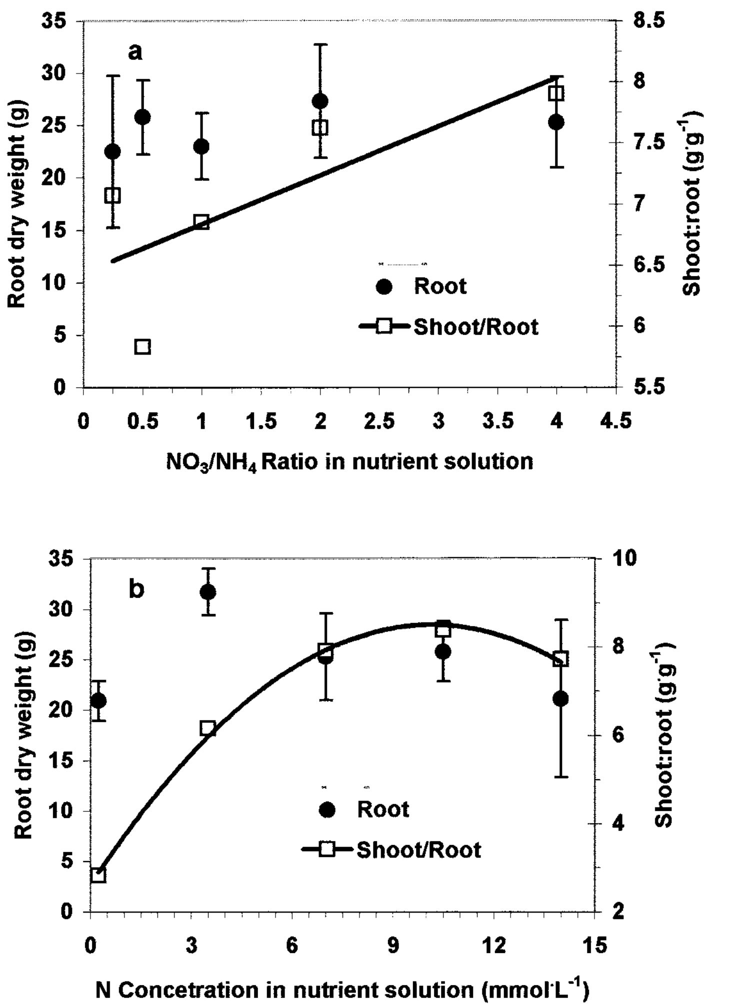

Fig. 2. Root dry weight and the shoot : root ratio at termination of the experiment (242 DAT) as a function of (**a**) $N\text{-}NO_3 : N\text{-}NH_4$ ratio (at a total N concentration of 7.0 $mmol{\cdot}L^{-1}$) and (**b**) total mineral N concentration (at a constant $N\text{-}NO_3 : N\text{-}NH_4$ ratio of 4.0). The equations of the lines and their parameters are presented in Table 2. Error bars present SE.

by flame photometer (Corning 400; Holstead Essex, U.K.), Ca and Mg concentrations by atomic absorption spectrophotometer (Perkin-Elmer 460, Norwalk, Conn.). NH_4 and NO_3 concentrations were determined with an injection Autoanalyzer (Lachat Instruments, Quichcem 8000, Milwaukee, Wis.).

The leaf chlorophyll content was determined spectrophotometrically at 652 nm after extraction of a weighed leaf disc (1 cm diameter) with 3 mL of N,N-dimethylformamide for 48 h at 4 °C in the dark (Moran and Porath, 1980). The optical density readings are transformed to $mg{\cdot}g^{-1}$ fresh weight using a standard curve.

The leaf soluble sugars and starch were determined in ethanol extraction of leaf discs. Five samples of leaf discs (each of 1-cm diameter) were extracted three times with 80% ethanol at 80 °C. The combined extracts were evaporated to dryness and redissolved in 2 mL distilled water, from which aliquots of 50–200 μL were taken for sugar determination. Reducing sugars were determined colorimetrically with dinitrosalicylic acid (Miller, 1959). Sucrose was measured by using the anthrone reagent method as modified for determination of non-reducing sugars (van Handel, 1968). Starch was determined by measuring glucose, following digestion of the ethanol-insoluble residue with amylglucoside (Dinar et al., 1983).

Data handling. Water uptake, U_w (L/ plant), was calculated as:

$$U_w = (W_{in} + W_m - W_f)/No \quad [1]$$

where W_{in} was the initial water volume in the container (L); W_m was the water volume added between successive replacements (L); W_f was the final water volume in the container at the end of the specified time interval (L), and No was the number of plants per container.

The transpiration rate, Tr ($L \cdot d^{-1}$), was calculated as:

$$Tr = U_w/t \quad [2]$$

where t was the specified time interval (d).

Total N ($NH_4 + NO_3$), potassium and calcium uptakes, U_i (g per plant), were calculated as:

$$U_i = (W_{in} * C_{iin} + W_m * C_{iW} - W_f * C_{if})/No \quad [3]$$

where i stands for N-NH_4, N-NO_3, K or Ca, C_{iin} was the initial element solution concentration ($g \cdot L^{-1}$); C_{iW} was the tap water ion concentration ($g \cdot L^{-1}$); and C_{if} was the final ion solution concentration at the end of the specified time interval ($g \cdot L^{-1}$).

The rates of element uptake, Q_i ($g \cdot d^{-1}$ per plant), were calculated as:

$$Q_i = U_i /t \quad [4]$$

The statistical analysis was carried out with the JMP software package (SAS Institute, Cary, N.C.); linear and quadratic regression were used to obtain the relations between solution N concentration or N-NO_3 : N-NH_4 ratio and plant variables. Each plot of one container was considered as one of the five replicates for the analysis of water and nutrient uptake; the pooled data of the four plants in each plot were used for plant organ DM production.

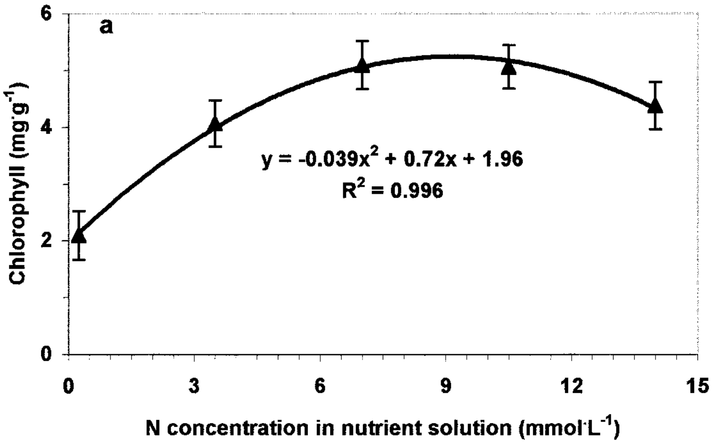

Fig. 3. Leaf chlorophyll concentration as a function of total mineral N concentration (at a constant N-NO_3 : N-NH_4 ratio of 4.0, 96 DAT). Error bars present SE.

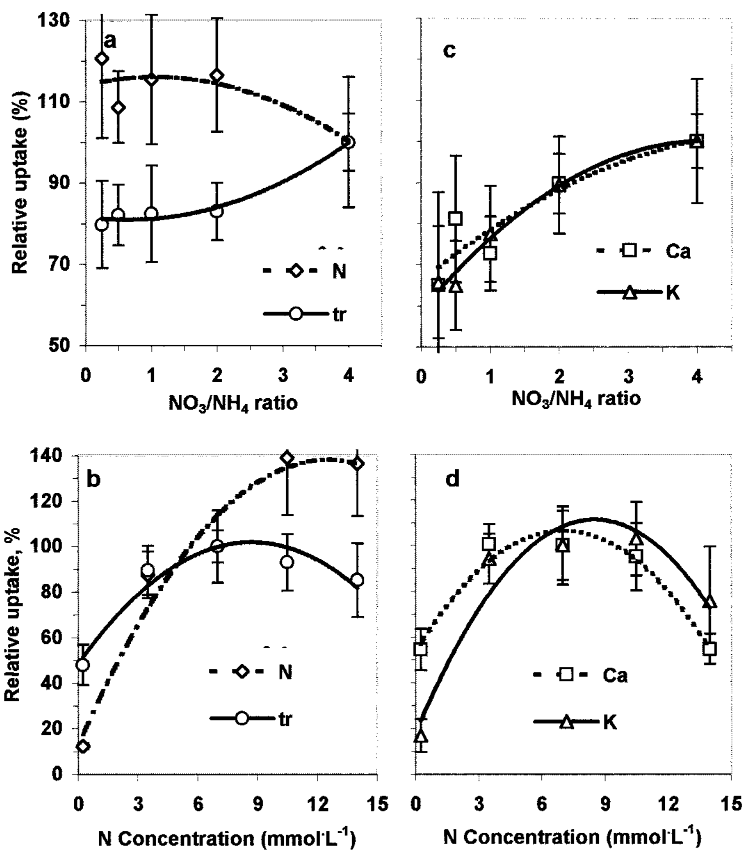

Fig. 4. The accumulated transpiration and minerals uptake expressed as relative values to a reference treatment (N = 7.0 $mmol \cdot L^{-1}$ and N-NO_3 : N-NH_4 = 4.0), (**a**) transpiration (tr) and N uptake (N) as functions of N-NO_3 : N-NH_4 ratio (at a total N concentration of 7.0 $mmol \cdot L^{-1}$), (**b**) transpiration (tr) and N uptake (N) as functions of total mineral N concentration (at a constant N-NO_3 : N-NH_4 ratio of 4.0), (**c**) Ca and K uptake as functions of N-NO_3:N-NH_4 ratio (at a total N concentration of 7.0 $mmol \cdot L^{-1}$) and (**d**) Ca and K uptake as functions of total mineral N concentration (at a constant N-NO_3 : N-NH_4 ratio of 4.0). The equations of the lines and their parameters are presented in Table 2. Error bars present SE.

Results

Dry matter production and plant growth. The N-NO_3 : N-NH_4 ratio in the studied range greatly affected stem and fruit DM while leaf DM was not affected (Fig. 1a). The effects of N-NO_3 : N-NH_4 ratio on fruit DM and stem were quadratic (Fig. 1a and Table 2). The calculated maximum of fruit and stem DM were obtained at N-NO_3 : N-NH_4 ratio of 3.7 and 3.5. However, Bar-Tal et al (2001) found that extending the N-NO_3 : N-NH_4 ratio to 9:1 did not reduce fruit yield.

The effect of N -NO_3 : N-NH_4 ratio on stem length was quadratic (Table 2), similar to its effect on stem weight. A response curve was fitted with the peak stem weight at a N-NO_3 : N-NH_4 ratio of 3.0. The short stems obtained with the low N-NO_3 : N-NH_4 ratios paralleled the occurrence of short internodes (data not shown). Wilcox et al. (1973) reported similar effect of N source on tomato plant morphology.

In contrast to the shoot DM, the final root DM was not affected significantly by the N-NO_3 : N-NH_4 ratio (Fig. 2a), unlike the reported high sensitivity of tomato roots to the N-NO_3 : N-NH_4 ratio (Ganmore-Neumann and Kafkafi, 1980a). In the vegetative phase of plant development, the root volume decreased as the N-NO_3 : N-NH_4 ratio increased (data not shown). Consequently, the shoot : root ratio increased linearly from 7.0 to 7.9 as the NO_3 : NH_4 ratio increased from 0.25 to 4.0 (Fig. 2 and Table 2).

The effect of N on stem, leaf, and fruit dry matter production as a function of N concentration was quadratic (Fig. 1b and Table 2). The calculated optimal N concentrations were 8.0 $mmol \cdot L^{-1}$ for the stem DM, and 9.2 and 9.4 $mmol \cdot L^{-1}$ for the leaf and fruit DM, respectively (Table 2). These values are within the range obtained for different open-field cultivars by Aloni et al. (1994). The effect of N concentration on stem length was quadratic, with the peak stem length at N concentrations of 7.3 $mmol \cdot L^{-1}$ (Table 2). The negative effects of the highest N concentration on fruit, leaf, and stem DM and on stem length are probably due to the increase in NH_4 concentration with increasing total N concentration. Unlike the strong effect of N concentration on shoot DM it had a small effect on root DM; just the maximal value of 31 g DM at a concentration of 3.5 $mmol \cdot L^{-1}$ was significantly different from the other treatments (based on analysis of variance analysis) (Fig. 2b). Consequently, shoot : root ratio increased sharply from 2.8 to 7.9 as N increased from

0.25 to 7.5 mmol·L^{-1} and the fitted curve for this ratio as a function of N concentration was quadratic, with a maximum value of 8.5 at 10.1 mmol·L^{-1}.

Chlorophyll, sugars and starch analysis. The N source (at a constant N concentration of 7 mmol·L^{-1}) had no significant effect on leaf chlorophyll and sugar and starch contents and similar results were obtained in another greenhouse experiment conducted in the following year (data not presented). The leaf chlorophyll content increased quadratically as the N concentration in the nutrient solution increased from 0.25 to 7.0 mmol·L^{-1} (at a constant N-NO_3 : N-NH_4 ratio of 4.0), (Fig. 3).

Transpiration. The effect of the solution N-NO_3 : N-NH_4 ratio on the transpiration was quadratic with a minimum value at a ratio of 0.65 (Fig. 4a and Table 2). In the studied range the total amount of transpired water during the growing season increased sharply with an increase in the N-NO_3 : N-NH_4 ratio from 2 to 4 (Fig. 4a). The effect of the highest NO_3 : NH_4 ratio on increasing the transpiration relative to the other treatments, started ≈3 months after transplanting and the difference increased steadily with time (Fig. 5a).

The effect of N concentration on the transpiration was quadratic with a maximum at 8.7 mmol·L^{-1} N (Fig. 4b and Table 2), similar to that of leaves and stem DM. The difference between the N treatments increased with time; the measured maximum transpiration was obtained with a solution N concentration of 7 mmol·L^{-1} (Fig. 5b) and the maximum daily transpiration rate was 1.6 L/d per plant, on 18 Apr. 232 DAT.

Nutrient uptake. The data collected in the experiment provided direct and indirect measurements of total nutrient uptake by the plants. Direct measurements were based on a chemical analysis of samples of plant organs, while indirect measurements were based on the weekly depletion of the nutrient from the culture solution. Bar-Tal et al., (1994) found good correlation between the two methods for nitrogen; in the present study the coefficients of correlation between the two methods for N, K, and Ca were 0.81, 0.86, and 0.87, respectively. Therefore, analysis of the uptake of nutrient as a function of time based on solution data (Eq. 3) is justified.

The effect of the solution N-NO_3 : N-NH_4 ratio on the relative U_N was different from its effects on transpiration (Fig. 4a). U_N decreased as the solution N-NO_3 : N-NH_4 ratio increased above 2.0. The effect of the N-NO_3 : N-NH_4 ratio on U_N was quadratic with the peak N uptake at a ratio of 1.1 (Fig. 4a and Table 2). This N-NO_3 : N-NH_4 ratio is much lower than the ratio for maximal dry matter production. The total N uptake vs. time was almost linear for all the NO_3 : NH_4 ratios from DAT 50 and on, however the slope varied between treatments. Therefore the difference between treatments increased with time (Fig. 6a).

Calcium uptake, U_{Ca}, increased quadratically as the N-NO_3 : N-NH_4 ratio increased throughout the studied range (Fig. 4c), the peak of U_{Ca} was calculated to occur at a ratio of

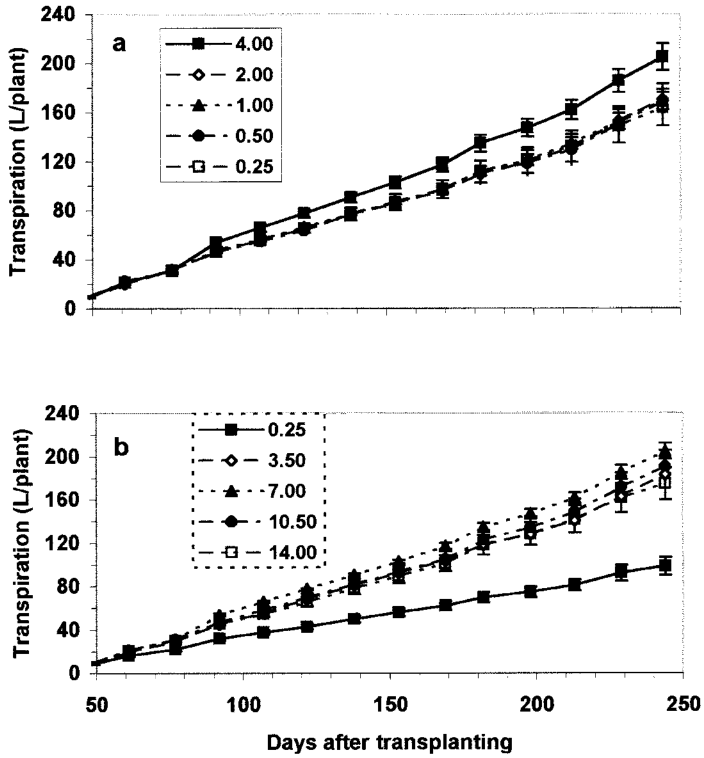

Fig. 5. Transpiration as a function of time and as affected by (**a**) NO_3 : NH_4 ratio (at a total N concentration of 7.0 mmol·L^{-1}) and (**b**) total mineral N concentration (at a constant N-NO_3 : N-NH_4 ratio of 4.0). Error bars present SE.

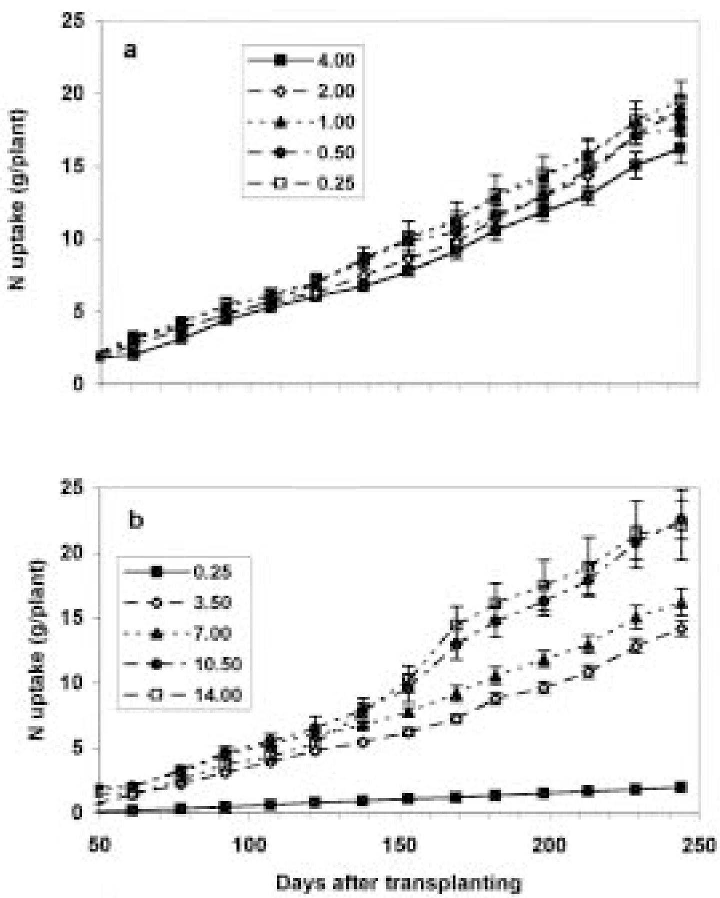

Fig. 6. N uptake as a function of time and as affected by (**a**) NO_3 : NH_4 ratio (at a total N concentration of 7.0 mmol·L^{-1}) and (**b**) total mineral N concentration (at a constant N-NO_3 : N-NH_4 ratio of 4.0). Error bars present SE.

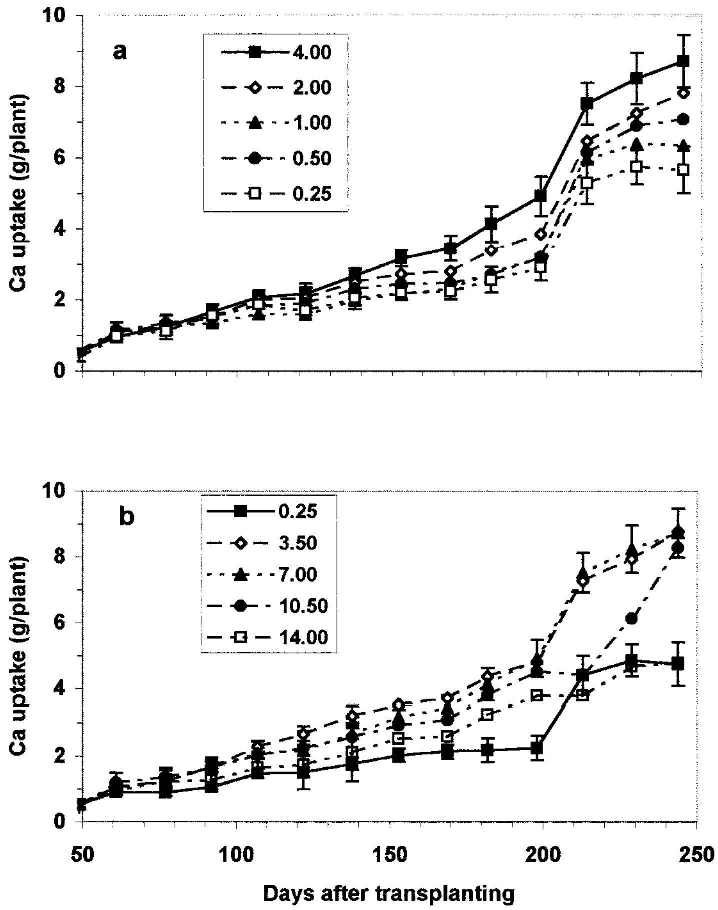

Fig. 7. Ca uptake as a function of time and as affected by (**a**) $NO_3 : NH_4$ ratio (at a total N concentration of 7.0 $mmol·L^{-1}$) and (**b**) total mineral N concentration (at a constant $N\text{-}NO_3 : N\text{-}NH_4$ ratio of 4.0). Error bars present SE.

5.3, beyond the range in this study (Table 2). These results are in agreement with the results of Marti and Mills (1991b). The relative increase in U_{Ca} as the $NO_3 : NH_4$ ratio increased from 0.25 to 2.0 was much bigger than that of the transpiration because of the competition between NH_4 and Ca. The accumulated Ca uptake vs. time was linear for all the $NO_3 : NH_4$ ratios between DAT 50 to 200, then the rate increased for all treatments because of a temporary increase in Ca concentration from 1.25 to 2.0 $mmol·L^{-1}$ in the supply water (Fig. 7a).

Potassium uptake, U_K, increased quadratically as the $N\text{-}NO_3 : N\text{-}NH_4$ ratio increased throughout the studied range (Fig. 4c), the peak of U_K was calculated to occur at a ratio of 4.1, beyond the range in this study (Table 2). The accumulated K uptake vs. time were almost linear for all the $N\text{-}NO_3 : N\text{-}NH_4$ ratios. However, because the slopes varied among treatments, the difference among treatments increased with time (Fig. 8a).

The N uptake, U_N, was the most responsive parameter to the solution N concentration; U_N increased quadratically with increasing the solution N concentration throughout the studied range (Fig. 4b), the peak of U_N , 22.4 g/plant, was calculated to occur at a solution N concentration of 12.5 $mmol·L^{-1}$ (Table 2). The difference among N treatments in the rate of N uptake increased with time; from 150 DAT (February) onwards, the total N uptake for N concentrations of 10.5 and 14.0 $mmol·L^{-1}$ was significantly larger than for N concentrations of 3.5 and 7.0 $mmol·L^{-1}$ (Fig. 6b).

The effect of the solution N concentration on Ca uptake (U_{ca}) was quadratic with a peak at a N concentration of 7.0 $mmol·L^{-1}$ (Fig. 4d and Table 2); this value is considerably lower than that for maximum transpiration and dry matter production. Ca uptake increased gradually until 200 DAT, after which there was a steep increase in U_{ca} (Fig. 7b), due to temporary increase in the Ca concentration in the supply water (uncontrolled by the research team).

The effect of the solution N concentration on K uptake (U_k) was quadratic with calculated peak at a N concentration of 8.5 $mmol·L^{-1}$ (Fig. 4d and Table 2). This value is similar to that of transpiration, higher than that of Ca, but much lower than that of N. The increase in U_k with increasing the solution N concentration from 0.25 to 3.5 $mmol·L^{-1}$ was similar to that of N and much greater than the increases in transpiration and Ca uptake (Fig. 4). The total uptake of K increased gradually from 50 DAT to the termination of the experiment; from 112 DAT onwards the total N uptake for N concentrations of 14.0 $mmol·L^{-1}$ was significantly smaller than for N concentrations of 3.5 to 10.5 $mmol·L^{-1}$ (Fig. 8b).

Discussion

Dry matter production and plant growth. The growth of greenhouse-grown pepper was found to be more sensitive to NH_4 fraction than that of tomato, as the optimal $N\text{-}NO_3 : N\text{-}NH_4$ ratios for shoot and root growth were 3.5 and 2.6, respectively, whereas an optimal ratio of ≈1.0 was found for tomato (Ganmore-Neumann and Kafkafi, 1980b). The increase in total yield with increasing the $N\text{-}NO_3 : N\text{-}NH_4$ ratio stemmed from the reduction in fruit physiological disorders, which reduced fruit mean weight (Bar-Tal et al. 2001). The N source had no considerable effect on leaf chlorophyll concentration. This finding contradicts published results on a reduction of pepper chlorophyll content by a high NH_4 fraction, where the total N concentration was 40 $mmol·L^{-1}$ (Takacs and Tecsi, 1992). Thus, the highest NH_4 concentration in that work was 30 $mmol·L^{-1}$, whereas 5.6 $mmol·L^{-1}$ was the highest concentration in the presented study. Also the sugar and starch contents in leaf and root were not affected by the $NO_3 : NH_4$ ratios.

Pepper growth was very responsive to N concentration in the range of 0.25 to 3·5 $mmol·L^{-1}$, the calculated maximum of fruit and leaf weights were obtained at a N concentration of 9.2-9.4 $mmol·L^{-1}$, and that of stem weight at a N concentration of 8.0 $mmol·L^{-1}$. These values are within the range of values previously found for various field (Aloni et al. 1994; Hartz et al., 1993) and greenhouse (Schon et. al., 1994; Qawasmi et al., 1999) grown pepper. The growth enhancement with increasing solution N concentration up to 10.5 $mmol·L^{-1}$, could be related to the increase in leaf chlorophyll content. The decrease in DM production as total N increased from 10.5 to 14.0 $mmol·L^{-1}$ may be related to the increase in NH_4 concentration from 2.1 to 2.8 $mmol·L^{-1}$ which reduced K and Ca uptake. In a similar way, the decrease in DM production as the $N\text{-}NO_3 : N\text{-}NH_4$ ratio decreased from 2.0 to 1.0 (at total N concentration of 7 $mmol·L^{-1}$) may be related to the increase in NH_4 concentration from 2.3 to 3.5 $mmol·L^{-1}$. Thus, the negative effect of N concentration above 10 $mmol·L^{-1}$ (at a $N\text{-}NO_3 : N\text{-}NH_4$ ratio of 4.0) may be attributed to the increase in NH_4 concentration.

The pattern of the effect of N concentration on the shoot : root ratio is similar to reported data for pepper seedlings (Bar-Tal et al., 1990a, b) and tomato (Thornley, 1972). This effect can be explained on the basis of competition or sink/source relationship between root and shoot. The root is the plant source for N, therefore a low N concentration in the nutrient solution restricts the shoot growth more than root growth (Brouwer and de Wit, 1968).

The retarding effect of high NH_4 fraction on stem growth was not related to chlorophyll and carbohydrates contents, in contrast to the suggested mechanism on the effect of NH_4 on carbohydrates consumption in strawberry (Ganmore-Neumann and Kafkafi, 1983). The observed effect of N on leaf chlorophyll content of pepper is consistent with published findings on the effects of N deficiency on chloroplast development and collapse by Thomson and Weier (1962a, b). Higher concentrations of sugars and starch were obtained in the lowest-N-concentration treatment, probably because of a lack of strong sinks, rather than higher production (data not presented).

Transpiration. The effect of the N-NO_3 : N-NH_4 ratio on transpiration (Fig. 4a) was much stronger than the effect on leaf weight (Fig. 1a), indicating that the N-NO_3 : N-NH_4 ratio had a specific effect on transpiration, probably through the change in the canopy morphology. The compact plants obtained with a low N-NO_3 : N-NH_4 ratio transpired less water, probably because the densely packed leaves reduced the radiation penetration and air flow, so the air layers around the leaves were more humid than those in the high NO_3:NH_4 ratio treatment.

The solution N concentration in the range of 3.5-14 mmol·L^{-1}, did not affect the rate of transpiration per unit leaf area (0.26 ± 0.046 mL·m^{-2}·s^{-1}), indicating that leaf area controlled the transpiration. Only with the lowest N concentration, 0.25 mmol·L^{-1}, a much higher transpiration rate per unit leaf area was obtained, probably because the severe N deficiency drastically reduced the leaf area index and water use efficiency. The fact that the treatment with the highest transpiration had the highest shoot : root ratio indicates that the root size did not limit transpiration.

Nutrient uptake. Decreasing the N-NO_3 : N-NH_4 ratio reduced the Ca and K uptakes, in agreement with previous findings in tomato (Ganmore-Neumann and Kafkafi, 1980b) and pepper (Marti and Mills, 1991a; 1991b), but enhanced that of N in contrast to the findings of Marti and Mills (1991a). This probably resulted from the rapid uptake of NH_4 under the conditions of constant pH as indicated by the rapid decline in the NH_4 concentration in the solution compared to that of NO_3 (data not presented). This is also the reason that high N concentration above 10.5 mmol·L^{-1} (containing 20% as N-NH_4 out of the total N) reduced cation uptake, transpiration, and stem length and weight.

The total N uptake of the treatment receiving N at 7 mmol·L^{-1} (at N-NO_3 : N-NH_4 ratio of 4.0, the treatment that produced the greatest high quality yield) was 16 g/plant, which is equivalent to 320 kg·ha^{-1} (two plants/m^2). This value is in reasonable agreement with data observed for the same cultivar in a commercial greenhouse, where the N uptake at 223 DAT was 10 g/plant or 330 kg·ha^{-1} (3.3 plants/m^2) (Tzipilevitz et al., 1996). One has to bear in mind that the presented study was a relatively short period of production; there would be an additional N consumption of ≈0.15 g/d/plant or 3 kg/d/ha for continuous production.

The total Ca uptake at the same treatment was 8.5 g/plant, equivalent to 170 kg·ha^{-1}, compared with 4 g/plant or 132 kg·ha^{-1} in commercial greenhouse (Tzipilevitz et al., 1996). The average daily Ca uptake rate for maximal yield for continuous production was ≈0.07 g/d/plant or 1.4 kg/ha/d. The increase in U_{ca} with increasing the N concentration from 0.25 to 3.5 mmol·L^{-1} is probably due to the increased transpiration and plant weight. The sharp reduction in U_{ca} as N concentration increased to 14 mmol·L^{-1} resulted probably because of competition between NH_4 and Ca.

The maximum K uptake in the highest-yielding treatments, was 26 g/plant, equivalent to 520 kg·ha^{-1}, compared with 12.5 g/plant or 412.5 kg·ha^{-1} in commercial greenhouses (Tzipilevitz et al., 1996). The daily K uptake rate for maximal yield under continuous production was 0.14 g/d/plant or 2.8 kg/ha/d. The slope of the U_k vs. time curve was almost constant for each treatment (Fig. 8), therefore, this is the daily uptake rate throughout the main season. The reduction in U_k as N concentration increased above 10.5 mmol·L^{-1} probably resulted from competition with NH_4.

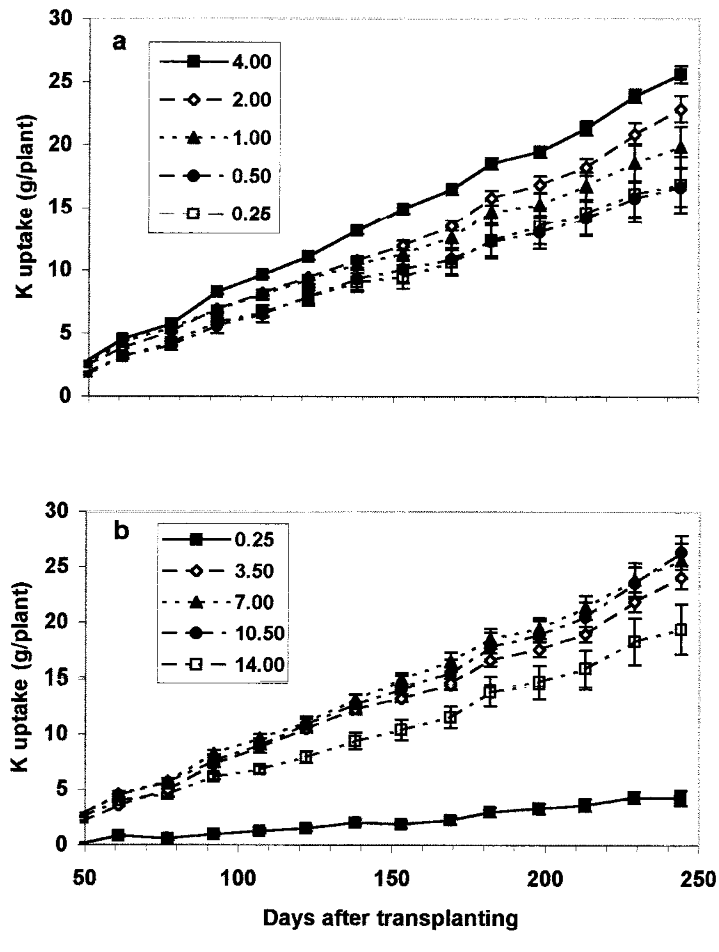

Fig. 8. K uptake as a function of time and as affected by (**a**) NO_3 : NH_4 ratio (at a total N concentration of 7.0 mmol·L^{-1}) and (**b**) total mineral N concentration (at a constant N-NO_3 : N-NH_4 ratio of 4.0). Error bars present SE.

Conclusions

The optimal N concentration for DM production of the different organs was 8.0–9.4 mmol·L^{-1}, whereas maximum high-quality yield was obtained at 8.2 mmol·L^{-1}. The negative effect of N concentration above 10 mmol·L^{-1} was probably caused by high NH_4 concentration as shown in Bar-Tal et al. (2001) and it coincided with the reduction in the uptake of Ca and K as N concentration increased above 7.0 mmol·L^{-1}.

Fruit and stem DM and plant height increased as the N-NO_3 : N-NH_4 ratio increased in the studied range (0.25 to 4.0), although this ratio had no significant effect on leaf weight and area. The optimum N-NO_3 : N-NH_4 ratio for maximum yield may be much higher as shown by Bar-Tal et al. (2001). The N-NO_3 : N-NH_4 ratio had a much larger effect on the shoot than root, indicating that the sensitivity of pepper to high NH_4 fraction is not related to root damage. The negative effect of low N-NO_3 : N-NH_4 ratio on fruit and vegetative organs DM production was not associated with damage to the chlorophyll or a reduction in carbohydrates. Total transpiration increased sharply as the N-NO_3 : N-NH_4 ratio increased from 2.0 to 4.0, probably as a result of the change in plant morphology. The effect of N-NO_3 : N-NH_4 ratio on N uptake was in the opposite direction of the effect on transpiration and DM production, indicating that the negative effect of a high NH_4 fraction is not related to N uptake. The patterns of the effects of N-NO_3 : N-NH_4 ratio on Ca and K uptakes indicate that the negative effect of high NH_4 fraction on DM production, fruit quality and the incidence of BER (Bar-Tal et al., 2001) were caused by unbalanced cations uptake.

The total uptake of N, Ca and K (of the treatment that produced the highest marketable yield, Bar-Tal et al., 2001) was 320, 170, and 520 $kg \cdot ha^{-1}$, respectively, and the maximum daily uptake rates were 3.0, 1.4 and 2.8 $kg \cdot ha^{-1}$, respectively.

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