JOURNAL OF PLANT NUTRITION, 21(9), 1879–1895 (1998)

Growth of a Tomato Crop at Reduced Nutrient Concentrations as a Strategy to Limit Eutrophication

M. Y. Siddiqi, H. J. Kronzucker, D. T. Britto, and A. D. M. Glass

Botany Department, University of British Columbia, Vancouver, B.C. V6T 1Z4, Canada

ABSTRACT

In tomato (*Lycopersicon esculentum* L. cv Trust F1), effects of various nutrient treatments on growth, fruit yield and quality, nutrient uptake and accumulation were studied in a hydroponic system. Reductions of macronutrient concentrations to 50% (0.5 x C) or 25% (0.25 x C) of the control (C) levels as well as cessation of replenishment of the feed solution for the last 16 days after 7 months growth at control levels, had no adverse effect on growth, fruit yield and fruit quality. However, reduction of macronutrient concentration to 10% of control (0.1 x C) reduced fruit yield by ~30%. Steady-state influx and net flux of NO_3^- into the roots of 4-6 week-old seedlings had not acclimated and showed concentration dependence from 1.1 mM (0.1 x C) to 11 mM (C). Whereas, Pi and K^+ fluxes were similar at 0.5 x C and C levels, at 0.1 x C they were significantly lower than the fluxes at higher concentrations, showing lack of acclimation at this concentration. This lack of flux acclimation may account for the adverse effects of low concentration (0.1 x C) on yield. The

results have been discussed in the context of eutrophication and it is suggested that in a non-recirculating hydroponic system, NO_3^-, Pi, and K^+ levels can be reduced to 25% of the concentrations currently being used in commercial greenhouses (C). In a recirculating system, the crop may be grown at control levels and used to deplete the feed solution for ~3 weeks prior to release of the solution to the drain.

INTRODUCTION

In order to optimize crop yield, both in the field and in greenhouses, crop species are provided with high levels of inorganic nutrients, e.g., lettuce (Pereira et al., 1989; Chen et al., 1997), bell pepper (D.L. Ehret, personal communication), tomato (Manrique, 1993). The consequences of applying such high amounts of nutrients are two-fold. Excessive levels of certain inorganic nutrients may be detrimental for plant growth. In lettuce, for example, growth was increased significantly when nitrate concentration of the feed solution was reduced from 9.6 mM (the level generally used in commercial greenhouses) to 0.96 mM (Chen et al., 1997). In tomatoes also, excessively high NO_3^- concentration (> 16 mM) may be detrimental for growth and fruit yield (Wilcox, 1962; Steiner, 1966; Adams et al., 1973; Gosselin et al., 1984). Perhaps more importantly, the environmental impact of the release of potentially eutrophying elements, e.g., NO_3^-, Pi to the ecosystem is a major concern globally. In commercial greenhouses, even in recirculating NFT (nutrient film technique) systems, disposal of the spent nutrient solutions poses a significant ecological problem. In non-recirculating hydroponic systems, the problem may be greatly exacerbated because of the potential for increasing the quantities of eutrophying elements released to ground waters, compared to the fully recirculating systems. It has been reported that an average greenhouse may release 1,000-4,000 L of solution (containing 900-3,600 kg fertilizers) per day (B.C. Ministry of Agriculture, 1994). That NO_3^- poses perhaps the greatest danger to the environment is only compounded by the fact that, due to plant requirements, it is present at higher concentrations than any other nutrient in the feed solutions. Because of environmental and health considerations, some countries have enacted legislation to limit NO_3^- levels in the drinking water, and in drainage water. In Canada, for example, the maximum NO_3^- concentration permitted in drinking water is 0.71 mM (B.C. Ministry of Agriculture 1994).

With these considerations in mind, we have investigated the extent to which the concentrations of macronutrients supplied to a tomato crop might be reduced without adversely affecting yield and quality of the fruits. In some pasture plants and crop species (e.g., ryegrass, barley, lettuce), NO_3^-, Pi, and K^+ in the feed solutions can be reduced to low μM concentrations without any adverse effects on growth and accumulation of these ions (Asher and Ozanne, 1967; Clement et al., 1978; Siddiqi and Glass, 1983a, 1983b; Glass and Siddiqi, 1984; Chen et al., 1997). In tomatoes, by contrast, the threshold values reported for NO_3^- concentration beyond

which growth failed to respond positively was 7-8 mM (Steiner, 1966; Gomez-Lepe and Ulrich, 1974; Wilcox and Magalhaes, 1985; Larouche et al., 1989).

In the present report, we describe the effects of reducing the levels of macronutrients to 50%, 25%, or 10% of the control levels (i.e., those used in commercial greenhouses) on plant growth and fruit yield in a fully recirculating hydroponic system. In another treatment, nutrient supply to one set of plants, hitherto growing at control concentrations, was withdrawn 16 days prior to the final harvest (i.e., prior to the disposal of the spent solution) with a view to allowing the tomato crop to reduce ambient concentrations of NO_3^-, Pi, and K^+ to concentrations that might be acceptably disposed to drains. The experiments described lasted 7-8 months. In addition, in short term (6 weeks) experiments, influx and net flux of NO_3^-, Pi, and K^+ were measured.

MATERIALS AND METHODS

Seed Germination and Plant Growth

Seeds of tomato (variety: Trust FI) were obtained from De Ruiter Seeds, Inc., St. Catharines, Ontario, Canada. These were germinated in rockwool plugs, moistened with the respective nutrient solutions (see below), for ~3 weeks. Rockwool plugs containing the seedlings were then placed in rockwool blocks, presoaked and subsequently watered regularly with the respective nutrient solutions. When plants were 6 weeks old, rockwool blocks containing the seedlings were transferred to black plastic pots (4-L capacity) filled to within two inches of the top with perlite. The top 5 cm were filled with pea gravel to minimize evaporation and to discourage algal growth. Each pot had a single drain-spout at a level which allowed ~1 L of standing solution at the bottom. The design of the pot ensured that the incoming irrigation solution mixed well with the standing solution before the excess drained off, via a PVC tube, back into the reservoir. The pots were also fitted with a tube to allow removal of samples from standing solutions at the bottom of the pots. These pots were placed in a completely recirculating system, and irrigated on a regular schedule from the top by pumping the respective aerated nutrient feed solutions from reservoirs (70-L capacity) by means of peristaltic pumps. The duration of this irrigation and the period between the irrigations were determined by monitoring nitrate, phosphate, and potassium concentrations of the standing solution at the bottom of the pots: concentrations of these ions were not allowed to fall below ~10% of prescribed concentrations. As plant demands for nutrients increased over time, it was necessary to reduce the interval between irrigations. This requirement was greatest for the 0.1 strength treatment (see below). However, adjustments in the irrigation time-table were made in all the treatments so that all other factors, e.g., oxygen status of the nutrient solution, moisture status in the pot would remain the same in all the treatments. Plants were grown for 7-8 months and fruits were continuously harvested as they turned light red in color. The

following parameters were determined: average diameter, shape, fresh weight. Based on these parameters, the quality of fruits was classified according to the British Columbia industry categories. These categories are based upon the size, shape, and whether the surface is smooth or blemished. The highest quality fruits are labeled gold, followed by white, #2, and cull (Greenhouse Growers' Cooperative Association, Surrey, BC). At the time of final harvest, fresh and dry weights of leaves and stems were also determined, as well as tissue elemental concentrations of the vegetative matter and fruits and other physical and chemical characteristics of the fruits, such as sugar content, total titratable acidity, and electrical conductivity of the pulp and firmness.

Nutrients Treatments

Two long-term experiments were carried out: one in 1994 (Experiment 1) and the other in 1995 (Experiment 2).

Experiment 1 (February 1994-September 1994)

In this experiment, 3 macronutrient treatment levels were applied: control (C), 50% of control (0.5 x C), and 10% of control (0.1 x C); micronutrients were at control level in all the treatments. Concentrations of NO_3^-, Pi, and K^+ were maintained at their respective levels by continuous infusion of appropriate stock solutions to the 70 L reservoirs by means of peristaltic pumps. The NO_3^- was provided as $Ca(NO_3)_2$, Pi as KH_2PO_4, and K^+ as KH_2PO_4, and K_2SO_4. All other nutrients were supplied in the same proportion to NO_3^- as in the original solution. Control levels, used by local commercial greenhouses, were as follows. Macronutrients (mM): NO_3^--N=11, $H_2PO_4^-$=0.8, SO_4^{2-}=4.1, Cl^-=1.0, K^+=8.0, Ca^{2+}=4.0, Mg^{2+}=2.5, Micronutrients (μM): Mn=7, B=50, Zn=4, Cu=0.75, Mo = 0.5, and Fe=20 (as Fe-DTPA). Each treatment consisted of 6 plants (replicates).

Experiment 2 (January 1995-September 1995)

In this experiment 3 treatments were applied: (a) control (C, as above), (b) plants were grown at Control levels until 16 days before the final harvest when the reservoir solution was allowed to deplete by withdrawing the supply of stock solutions (16-day depletion treatment), and (c) 25% of control (0.25 x C). Each treatment consisted of 6 plants.

Short-Term Experiments

Plants were rooted directly in a large volume (76 L) of nutrient solution which was aerated and continuously mixed. This set procedure was adopted for two reasons: (a) to ensure that all the roots were bathed in nutrient solutions in which concentrations of nutrients were maintained at the desired levels; (b) to obtain a

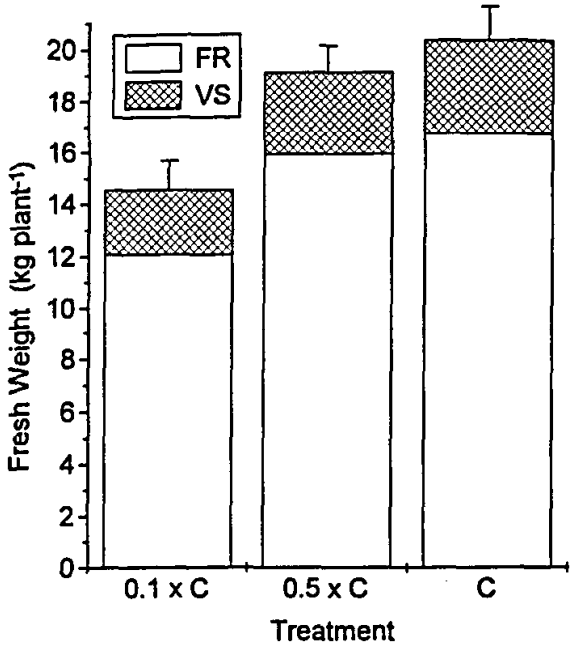

FIGURE 1. Fresh weight of fruits (FR) and shoots (VS) per plant as functions of external macronutrient concentrations in Experiment 1. C = Control, 0.1 x C = 10% of Control, 0.5 x C = 50% of Control (see text and Table 1).

relatively large number of seedlings with which to measure short-term unidirectional influxes and net fluxes of NO_3^-, Pi, and K^+.

Measurement of Fluxes

Unidirectional influxes of NO_3^-, Pi, and K^+ into the intact roots of seedlings were measured under steady state conditions. The roots were exposed to the appropriate solutions labeled with $^{13}NO_3^-$, $H_2{}^{32}PO_4^-$, or $^{86}Rb^+$ for 10 min. Before the exposure to the radiotracer, roots were prewashed for 5 min in an identical but non-radioactive solution. Influx was terminated by a 2 min wash ($^{13}NO_3^-$ experiments) or 5 min wash ($H_2{}^{32}PO_4^-$, or $^{86}Rb^+$ experiments) of roots in an identical but non-radioactive solution to remove the radiotracer from the apparent free space (Siddiqi and Glass, 1983b; Siddiqi et al., 1989). Roots and shoots were separated and counted in a γ-counter (^{13}N), or in a scintillation counter (^{32}P and ^{86}Rb).

Soluble Sugars

Total soluble sugars were measured by the anthrone method. In brief, sliced tomato fruit was homogenized in a milk shake mixer and filtered through 2 layers of

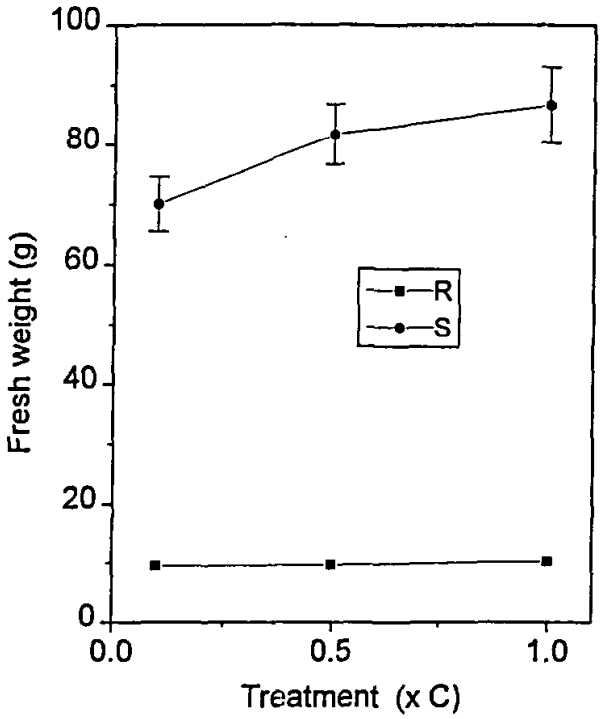

FIGURE 2. Fresh weights of shoots and roots per plant as functions of external macronutrient concentrations in a short-term (6 weeks) experiment. C = Control, 0.1 x C = 10% of Control, 0.5 x C = 50% of Control (see text and Figure 1).

cheese-cloth. The filtrate (15 mL), henceforth referred to as "pulp" was taken in a preweighed centrifuge tube, diluted by adding 10 mL distilled water and its weight determined. It was then centrifuged at 1,000 x g for 10 min. The supernatant was collected in a test tube and its volume and weight determined. After appropriate dilution of the supernatant, soluble sugars were measured colorimetrically by adding concentrated HCl, 45% formic acid, and anthrone/sulphuric acid solution. The absorbance was read at 630 nm in a Phillips PU 8820 U.V./visible spectrophotometer.

Titratable Acidity

A known volume of the pulp (50 mL) was taken in a beaker, weighed and its pH recorded. It was then titrated with 1M NaOH to pH 7 while continuously stirring. Total titratable acidity was expressed as the amount of 1M NaOH (mL) required to neutralize 50 mL of the pulp.

Electrical Conductivity

Electrical conductivity of the pulp was measured by use of a portable conductivity meter (HANNA Instruments, HI 8033).

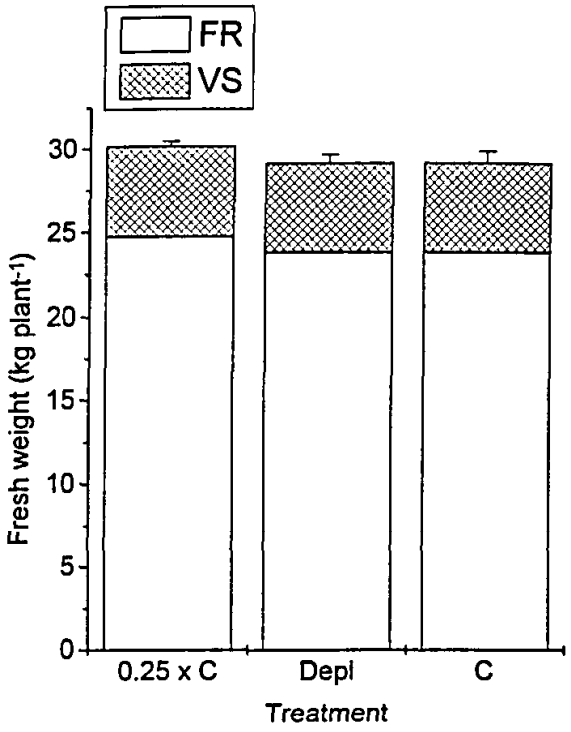

FIGURE 3. Fresh weight of fruits (FR) and shoots (VS) per plant as functions of external macronutrient concentrations from Experiment 2. C = Control, 0.25 x C = 25% of Control, Depl= Plants grown under Control conditions until 16 days prior to the final harvest when replenishment of nutrients was stopped (16-day depletion treatment, see text and Table 2).

Firmness

Firmness of the fruit was measured as the deformation of the surface when a known force (3 Kg) was applied to the fruit for 20 seconds. The results were expressed as: % deformation=deformation x 100/diameter of the fruit.

RESULTS AND DISCUSSION

Growth and Fruit Yield

There was no significant effect on plant growth and fruit yield when concentrations of macronutrients in the feed solution were reduced to 50% (0.5 x C, Experiment 1) or 25% (0.25 x C, Experiment 2) of the control (C) or when plants were grown at control levels but the feed solution was allowed to deplete for the last 16 days before the final harvest (16-day depletion, Experiment 2) (Figures 1-3). These treatments (0.5 x C, 0.25 x C, and 16-day depletion), caused no adverse effects on the quality of fruits, as determined by morphological attributes, e.g., size, shape, appearance (Table 1), elemental composition (Table 2), firmness, dry matter, soluble

TABLE 1. Fresh weight of fruits of various grades (kg plant^{-1}) and number of fruits (in parentheses) as a function of external concentration of macronutrients. Control (C) is the level used in commercial greenhouses (see text). In half (0.5xC)-, quarter (0.25xC)-, and tenth (0.1xC)- treatments, concentrations of macronutrients were reduced to 50%, 25%, and 10% of the control, respectively. In supply-stopped (16-day depletion) treatment, plants were grown at control levels but nutrients removed by plant uptake were not replenished during the last 16 days.

(a) Experiment 1

	Fruit Grade				
Treatment	Gold	White	# 2	Cull	Unripe
Control (C)	7.81 (38)	4.13 (20)	1.28 (7)	1.21 (6)	2.31 (21)
0.5 x C	7.94 (37)	4.23 (19)	0.95 (6)	0.10 (1)	2.72 (21)
0.1 x C	5.43 (28)	2.99 (18)	0.79 (4)	0.63 (5)	2.24 (20)
F-ratio	5.25 (5.73)	2.53 (0.25)	1.48 (1.52)	5.31 (3.74)	1.08 (1.02)
Probability (P)	< 0.05	N.S.	N.S.	< 0.05 *	N.S.

* Bartlett's X^2 significant

(b) Experiment 2

	Fruit Grade				
Treatment	Gold	White	# 2	Cull	Unripe
Control (C)	16.8 (76)	1.52 (7)	1.44 (8)	0.92 (6)	3.2 (29)
ST	16.8 (73)	1.32 (6)	1.13 (7)	1.35 (9)	3.3 (29
QT	16.5 (72)	2.04 (9)	0.98 (6)	1.40 (8)	3.9 (30)

Differences between treatments were not significantly different (P>0.05).

sugars, acidity, and electrical conductivity of the juice (Table 3). It is noteworthy that in 0.25 x C (Experiment 2), NO_3^- concentration of the feed solution (2.4 mM) was much lower than the hitherto reported threshold concentrations (7-8 mM) below which fruit yield has been reported to be reduced (Steiner, 1966; Wilcox and Magalhaes, 1985; Larouche et al., 1989). These differences in the threshold concentrations may reflect varietal differences or environmental conditions (e.g., temperature, day length). In some species (e.g., barley or wheat), substantial varietal differences in the rates of uptake and utilization of nutrients such as K^+, NO_3^-, have been found (Glass and Perley, 1980; Siddiqi and Glass, 1983a, 1983b; Perby and Jensen, 1983, 1984; Woodend et al., 1987; Woodend and Glass, 1993).

TABLE 2. Inorganic macronutrient concentrations in the tissues (% dry weight ± s.e.) as a function of external concentration of macronutrients. Control (C) is the level used in commercial greenhouses (see text). In half (0.5xC)-, quarter (0.25xC-), and tenth (0.1xC)-treatments, concentrations of macronutrients were reduced to 50%, 25%, and 10% of the control, respectively. In supply-stopped (16-day depletion) treatment, plants were grown at control levels, but nutrients removed by plant uptake were not replenished during the last 16 days.

(a) Experiment 1

	Macronutrients (% dry weight)				
Treatment	N	P	K	Ca	Mg
FRUITS					
Control (C)	2.1 ± 0.1	0.50 ± 0.02	3.7 ± 0.1	0.16 ± 0.01	0.11 ± 0.01
0.5 x C	2.0 ± 0.1	0.52 ± 0.05	3.8 ± 0.1	0.17 ± 0.02	0.12 ± 0.01
0.1 x C	2.0 ± 0.1	0.45 ± 0.02	3.5 ± 0.1	0.20 ± 0.01	0.13 ± 0.01
VEGETATIVE SHOOT (leaf + stem)					
Control (C)	4.3 ± 0.2	1.05 ± 0.06	3.3 ± 0.1	4.7 ± 0.2	0.88 ± 0.05
0.5 x C	3.6 ± 0.3	1.24 ± 0.16	3.6 ± 0.1	5.1 ± 0.4	0.86 ± 0.1
0.1 x C	3.7 ± 0.2	0.68 ± 0.07	3.3 ± 0.3	4.9 ± 0.7	0.73 ± 0.06

(b) Experiment 2

	Macronutrients (% dry weight)				
Treatment	N	P	K	Ca	Mg
FRUITS					
Control (C)	1.9 ± 0.1	0.56 ± 0.01	3.7 ± 0.1	0.20 ± 0.01	0.12 ± 0.01
8-d depletion	1.7 ± 0.0	0.55 ± 0.02	3.5 ± 0.1	0.21 ± 0.01	0.12 ± 0.01
16-d depletion	1.7 ± 0.1	0.54 ± 0.02	3.5 ± 0.1	0.23 ± 0.02	0.12 ± 0.01
0.25 x C	1.8 ± 0.1	0.60 ± 0.01	3.7 ± 0.1	0.23 ± 0.01	0.12 ± 0.01
VEGETATIVE SHOOT (leaf + stem)					
Control (C)	3.9 ± 0.1	1.12 ± 0.18	3.4 ± 0.1	5.3 ± 0.3	0.73 ± 0.32
16-d depletion	2.9 ± 0.1	0.63 ± 0.08	2.8 ± 0.1	3.9 ± 0.3	0.66 ± 0.03
0.25 x C	3.6 ± 0.2	1.08 ± 0.06	3.0 ± 0.1	4.7 ± 0.2	0.76 ± 0.03

TABLE 3. Chemical and physical characteristics of fruits as a functions of external concentrations of macronutrients: soluble sugars (%), titratable acidity (mL of 1M NaOH to neutralize pH of 50mL juice), pH, and Firmness (% deformation). Control (C) is the level used in the commercial greenhouses (see text). In supply-stopped (16-day depletion) treatment plants were grown at control levels, but the solutions were allowed to deplete for the last 16 days. In quarter (0.25%xC)- treatment, concentrations of macronutrients were reduced to 25% of the control (see text). Fruits were harvested and analyzed from all treatments 8 and 16 days after withdrawal of nutrient supply to the 16-day depletion treatment.

	Fruit Characteristic				
Treatment	Sugars	Acidity	pH	E.C.	Firmness
(a) Measured 8 days after withdrawl of nutrient supply to ST treatment (ST-8).					
Control (C)	4.1 ± 0.2	1.66 ± 0.03	4.67 ± 0.01	2.53 ± 0.05	ND*
8-depletion	4.1 ± 0.1	1.66 ± 0.03	4.66 ± 0.02	2.55 ± 0.05	ND*
0.25 x C	4.2 ± 0.2	1.68 ± 0.03	4.65 ± 0.02	2.52 ± 0.06	ND*
(b) Measured 16 days after withdrawl of nutrient supply to a Control treatment.					
Control (C)	4.3 ± 0.2	1.61 ± 0.01	4.59 ± 0.01	2.50 ± 0.02	9.9 ± 0.5
16-d depletion	4.1 ± 0.2	1.63 ± 0.01	4.61 ± 0.01	2.50 ± 0.04	9.3 ± 0.4
0.25 x C	4.1 ± 0.2	1.69 ± 0.03	4.60 ± 0.01	2.47 ± 0.02	9.4 ± 0.6

*Not determined.

In a recirculating hydroponic system, it is at the time of disposal to the drain that the high concentrations of eutrophying elements in the feed solution enter the environment. Clearly then, in such a system, the 16-day depletion strategy (Experiment 2) may be preferable since, although lower concentrations have no adverse effects on yield, their maintenance in a recirculating system may not be as easy as that of control. By contrast, in non-recirculating systems where maintenance of concentrations is not a factor, application of the lowest concentration, without compromising yield, can be achieved.

Interestingly, while elemental concentrations of the vegetative matter were not affected by provision of reduced macronutrient concentrations (0.5 x C and 0.25 x C treatments, Experiments 1 and 2, respectively), concentrations of total nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) were substantially reduced when the feed solution was allowed to deplete for 16 days (16-day depletion, Experiment 2) (Table 2). Evidently, fruit loading occurred at the cost of the leaves since the latter treatment caused only a very minor reduction in the elemental composition of the fruits.

TABLE 4. Steady-state influxes (10 min) of $^{13}NO_3^-$, ^{32}Pi, and $^{86}Rb^+$ - K^+ into the roots 4- or 5-week-old seedlings of Trust tomato (μmol g^{-1} root fwt h^{-1}), isotope tranlocated to the shoot (% of total isotope absorbed in 10 min), and NO_3^-, Pi, and K^+ concentrations of roots and shoots (μmol g^{-1} root fwt h^{-1}) in plants grown at control or 0.05xC or 0.1xC levels of macronutrients (see text).

Treatment	Influx (μmol g^{-1} h^{-1})	Isotope in shoot (%)	$[ion]_i$ (μmol g^{-1}) Roots	Shoot
(a) $^{13}NO_3^-$ Influx into 4 week-old seedlings				
Control	13.22 ± 1.08	51 ± 2	38.9 ± 1.2	40.2 ± 2.3
0.5 x C	7.86 ± 0.65	50 ± 1	37.3 ± 1.4	38.1 ± 1.5
0.1 x C	2.39 ± 0.18	33 ±2	29.3 ± 1.8	32.5 ± 0.1
(b) ^{32}Pi Influx into 5 week-old seedlings				
Control	0.72 ± 0.06	11 ± 1	14.7 ± 2.0	12.6 ± 1.5
0.5 x C	0.96 ± 0.13	6 ± 1	14.5 ± 0.2	13.4 ± 0.3
0.1 x C	0.41 ± 0.05	9 ± 1	15.1 ± 0.1	15.2 ± 2.5
(c) ^{86}Rb - K^+ Influx into 5 week-old seedlings				
Control	5.25 ± 0.20	37 ± 1	68.4 ± 2.4	111.0 ± 4.3
0.5 x C	6.23 ± 0.32	36 ± 2	80.3 ± 2.8	97.9 ± 1.9
0.1 x C	2.50 ± 0.16	28 ± 2	81.0 ± 6.4	99.3 ± 9.7

However, plant growth and fruit yield were substantially reduced (by ~30%) when the concentrations of macronutrients in the feed solution were lowered to 10% of control (0.1 x C, Experiment 1) (Figures 1 and 2 and Table 1a). In the case of fruits in 0.1 x C, yields of all morphologically based categories declined to a similar extent (Table 1a), but there was little change in physical and chemical characteristics of the fruits or vegetative matter (data not shown). Clearly, tomato contrasts sharply with other plants studied, in which reduction of nutrient concentrations even to low μM concentrations caused no reduction of growth, e.g., pasture species (Asher and Ozanne, 1967), ryegrass (Clement et al., 1978), barley (Siddiqi and Glass, 1983a), lettuce (Chen et al., 1997). This acclimation appears to result from up-regulation of nutrient uptake by plant roots as well as increases of root biomass. Thus nutrient acquisition may become independent of external concentration. However, in the present case, short term NO_3^-, Pi and K^+ influx and net uptake rates, in contrast to the findings of the latter studies, had not acclimated to reductions in external concentrations in tomato during the early stages of growth (Tables 4 and 5). It is noteworthy that the concentrations of these ions in the roots and shoots were similar among the treatments (Table 4). Thus, these differences among the steady-state fluxes were independent of any control exerted by tissue ion concentration. Tomato differs from barley, ryegrass and lettuce (which show acclimation of fluxes, as mentioned above) in that its growth is indeterminate and that it has a relatively large sink in terms of leaves and fruits. It may also be that, in

TABLE 5. Net uptake (measured over 6 hours) of NO_3^-, Pi, and K^+ (μmol g^{-1} root fwt h^{-1}) by 6-week-old seedlings of Trust tomato, grown at control.

	Net Flux (μmol g^{-1} root fwt h^{-1})		
Treatment	NO_3^-	Pi	K^+
Control (C)	21.3 ± 2.4	1.15 ± 0.11	11.74 ± 1.60
0.5 x C	14.3 ± 0.4	1.11 ± 0.02	7.63 ± 0.55
0.1 x C	7.5 ± 1.1	0.72 ± 0.06	3.27 ± 0.31

tomato, there is a substantial transpiration-dependent uptake of nutrients, bypassing symplastic loading (e.g., Pitman, 1977).

In 0.1 x C (Experiment 1), blossom end rot, which is generally associated with Ca^{2+} deficiency, was observed on some fruits on the first truss only. It should be noted that in the treatments described, concentrations of macronutrients were established in 70 L reservoirs at the start of the experiment. Subsequently, only the concentrations of NO_3^-, Pi, and K^+ were monitored daily and maintained at the prescribed levels. Other nutrients were supplied together with N, P, K, in a fixed

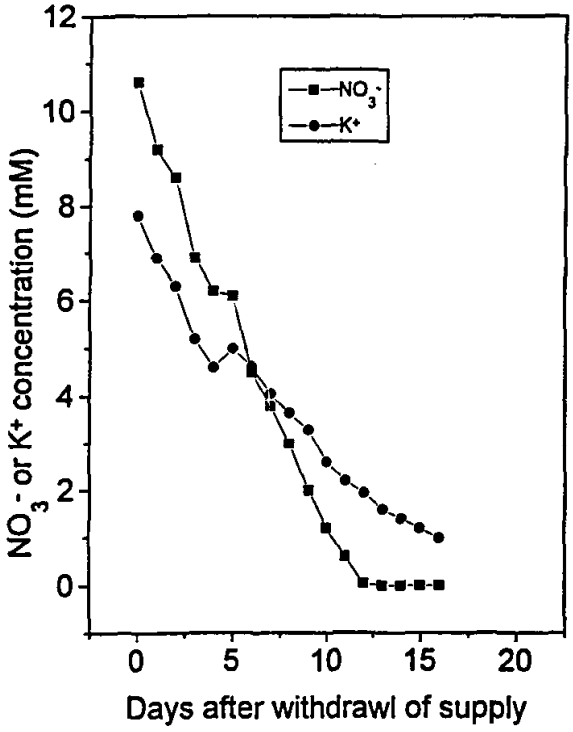

FIGURE 4. Depletion of nitrate and potassium in the nutrient solution from control levels (day 0) over 16 days from Experiment 2 (16-day depletion treatment, see text).

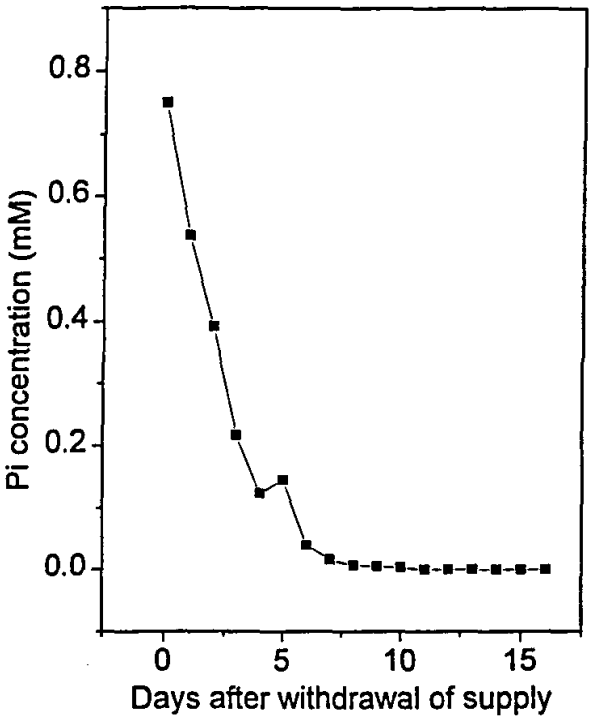

FIGURE 5. Depletion of phosphate in the nutrient solution from control levels (day 0) over 16 days from Experiment 2 (16-day depletion treatment, see text).

ratio, according to the depletion rate of NO_3^-. A complete elemental analysis half way through the experiment showed that the concentrations of some nutrients, e.g., Ca^{2+}, had increased several fold: ~2-3 times in control to ~10 times in the lowest concentration (0.1 x C) treatment. It is probable that the source of the noted blossom end rot in the 0.1 x C treatment was due to inadequate Ca^{2+} levels during the early part of the experiment. Subsequently, however, as Ca^{2+} levels increased sufficiently, blossom end rot was remedied and not observed on the fruits past the first truss.

Depletion of Feed Solution

Figures 4-6 show the patterns of depletion of NO_3^-, Pi, K^+, and the corresponding decline of E.C. after terminating the replenishment of feed solution (Experiment 2). Nitrate and Pi levels were reduced from Control to virtually zero within ~2 weeks of withdrawing supply of nutrients to the reservoir; however, K^+ concentration was still ~ 1 mM at the end of the experiment (after depletion for 16 days). Clearly, the rate at which nutrients are depleted under these conditions will be a function of plant size, number of plants and reservoir volume. In the present case, plants were 8 months old and reservoir volume:plant number ratio was 12 L:1 plant. Table 6

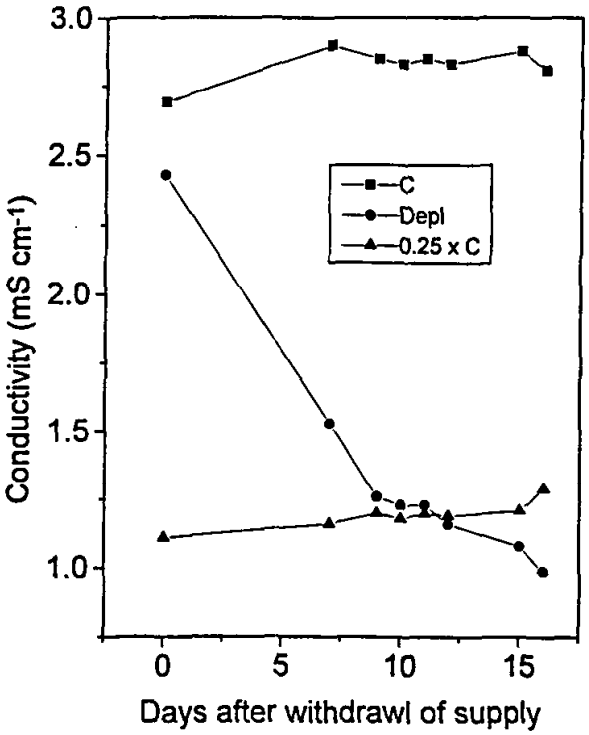

FIGURE 6. Electrical conductivity of the feed solutions during the last 16 days before the final harvest from Experiment 2. C = Control, 0.25 x C = 25% of control, Depl = Plants grown under Control conditions until 16 days prior to the final harvest when replenishment of nutrients was stopped (16-day depletion treatment, see text)

TABLE 6. Amounts of nitrate, phosphate, and potassium in the reservoirs (70 L each) and depletion rates of these ions by 6 plants during the last 3 weeks of growth (Experiment 1) under conditions of continuous replenishment of nutrients (see text).

	In reservoir (mmol)			Depletion rate (mmol d^{-1})		
Treatment	NO_3^-	Pi	K^+	NO_3^-	Pi	K^+
Control (C)	770	56	560	128	27	72
0.5 x C	385	28	280	99	19	60
0.1 x C	77	5.6	56	81	10	47

shows the rates of uptake of these nutrients for the corresponding period (last 3 weeks) from Experiment 1 when the feed solutions were continuously replenished. Note that the rates of depletion from Experiment 1 (Table 6) and Experiment 2 (Figure 4) agree well.

CONCLUSIONS

1. In a recirculating hydroponic system, NO_3^-, Pi, and K^+ concentrations can be reduced to 25% strength (0.25 x C) without adverse effects on yield or fruit quality. In non-recirculating systems, this strategy would substantially reduce the release of nitrate and phosphate to the environment.
2. In recirculating systems, an alternate strategy may be to maintain nutrient concentrations at control levels and reduce them prior to release to the environment by terminating the replenishment of nutrients in the reservoir solution ~2-3 weeks prior to the final harvest.
3. We suggest that concentrations of individual ions (particularly those of NO_3^- and Pi), rather than EC, be maintained. Because the supply of some nutrients, e.g., Ca^{2+}, Mg^{2+}, SO_4^{2-}, exceeded absorption, concentrations of these nutrients increased in recirculating solution over time. As a consequence, the contribution of these ions to electrical conductivity caused this parameter to increase from 2.08 to 3.46 mS cm^{-1} in C, from 0.95 to 2.25 mS cm^{-1} in 0.5 x C, and from 0.35 to 1.46 mS cm^{-1} in 0.1 x C (Experiment 1). Growers who maintain E.C. may be doing so at the expense of NO_3^-, Pi, and/or K^+ concentrations which may be declining despite the constancy of measured E.C.

ACKNOWLEDGMENTS

We wish to thank the following for their help in many different forms: Mr. Jim Portree (B.C. Ministry of Agriculture), Mr. Joseph J. Vidmar (Botany, University of B.C.), Dr. David Ehret, Dr. Wei Lin, Mr. Glen Block (Agriculture Canada), Mr. Brian Mauza (Greenhouse Grower's Association of BC), Mr. David Ryall, and Mr. Armand Van der Meulen. We wish to record our appreciation for DuRuiters Seeds, Inc., who generously provided the seeds as a gift throughout this study. Financial support for this work from Canada/B.C. Green Plan and B.C. Vegetable Growers' Cooperative is gratefully acknowledged.

REFERENCES

Adams, P., G.W. Winsor, and J.D. Donald. 1973. The effect of nitrogen, potassium, and subirrigation on the yield, quality, and composition of single-truss tomatoes. J. Hort. Sci. 48:123-133.

Asher, C.J. and P.G. Ozanne. 1967. Growth and potassium content of plants in solution cultures maintained at constant potassium concentrations. Soil Sci. 103:155-161.

B.C. Ministry of Agriculture. 1994. Environmental Guidelines for Greenhouse Growers in British Columbia. B.C. Ministry of Agriculture, Fisheries and Food, Resource Management Branch, Abbotsford, BC, Canada.

Chen, X.G., C. Gastaldi, M.Y. Siddiqi, and A.D.M. Glass. 1997. Growth of a lettuce crop at low ambient nutrient concentrations: A strategy designed to limit the potential for eutrophication. J. Plant Nutr. 20:1403-1417.

Clement, C.R., M.J. Hopper, and L.H.P. Jones. 1978. The uptake of nitrate by *Lolium perenne* from flowing nutrient solutions. I. Effect of NO_3^- concentration. J. Exp. Bot. 29:453-464.

Glass, A.D.M. and J.E. Perley. 1980. Varietal differences in potassium uptake by barley. Plant Physiol. 65:160-164.

Glass, A.D.M. and M.Y. Siddiqi. 1984. The control of nutrient uptake rates in relation to the inorganic composition of plants. Adv. Plant Nutr. 1:103-147.

Gomez-Lepe, B.E. and A. Ulrich. 1974. Influence of nitrate on tomato growth. J. Am. Soc. Hort. Sci. 99:45-49.

Gosselin, A., M.J. Trudel, F.P. Chalifour, and G. Gendron. 1984. Influence de la temperature du substrat et de la fertilization azotee sur la croissance, le development, la teneur en azotee et l'activite nitrate reductase de plants de tomate. Can J. Plant Sci. 64:181-191.

Larouche, R., L. Vezina, and A. Gosselin. 1989. Nitrogen concentration and photosynthetic photon flux in greenhouse tomato production. I. Growth and development. J. Am. Soc. Hort. Sci. 114:458-461.

Manrique, L.A. 1993. Greenhouse crops: A review. J. Plant Nutr. 16:2411-2477.

Perby, H. and P. Jensen. 1983. Varietal differences in uptake and utilization of nitrogen and other macro-elements in seedlings of barley, *Hordeum vulgare*. Physiol. Plant. 58:223-230.

Perby, H. and P. Jensen. 1984. Net uptake and partitioning of nitrogen and potassium in cultivars of barley during ageing. Physiol. Plant. 61:559-565.

Pereira, N.N.C., M.S. Fernandes, and D.L.D. Almeida. 1989. Nitrogen nutrition for lettuce: Effects of nitrogen carriers and nitrification inhibition. Pesquisa Agropeuaria Brasileira 24:647-654.

Pitman, M.G. 1977. Ion transport into the xylem. Annu. Rev. Plant Physiol. 28:71-88.

Siddiqi, M.Y. and A.D.M. Glass. 1983a. Studies of the growth and mineral nutrition of barley varieties. I. Effect of potassium supply on the uptake of potassium and growth. Can. J. Bot. 61:671-678.

Siddiqi, M.Y. and A.D.M. Glass. 1983b. Studies of the growth and mineral nutrition of barley varieties. II. Potassium uptake and its regulation. Can. J. Bot. 61:1551-1558.

Steiner, A.A. 1966. The influence of the chemical composition of a nutrient solution on the production of tomato plants. Plant Soil 24:454-466.

Wilcox, G.E. 1962. Tomato response to nitrogen fertilization in Indiana. Indiana Acad. Sci. 72:300-306.

Wilcox, G.E., J.R. Magalhaes, and F.L.I.M Silva. 1985. Ammonium and nitrate concentrations as factors in tomato growth and nutrient uptake. J. Plant Nutr. 8:989-998.

Woodend, J.J. and A.D.M. Glass. 1993. Inheritance of potassium uptake and utilization in wheat (*T. aestivum* L.) grown under potassium stress. J Genet. & Breed. 47:95-102.

Woodend, J.J., A.D.M. Glass, and C.O. Person. 1987. Genetic variation in the uptake and utilization of potassium in wheat (*Triticum aestivum* L.) varieties grown under potassium stress. pp. 383-391. In: H.W. Gabelman and B.C. Loughman (eds.), Genetic Aspects of Plant Nutrition. Martinus Nijhoff, Dordrecht, The Netherlands.