



## Effects of elevated CO<sub>2</sub> concentration on growth and water usage of tomato seedlings under different ammonium/nitrate ratios

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### Abstract

Increasing atmospheric CO<sub>2</sub> concentration is generally expected to enhance photosynthesis and growth of agricultural C<sub>3</sub> vegetable crops, and therefore results in an increase in crop yield. However, little is known about the combined effect of elevated CO<sub>2</sub> and N species on plant growth and development. Two growth-chamber experiments were conducted to determine the effects of NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratio and elevated CO<sub>2</sub> concentration on the physiological development and water use of tomato seedlings. Tomato was grown for 45 d in containers with nutrient solutions varying in NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratios and CO<sub>2</sub> concentrations in growth chambers. Results showed that plant height, stem thickness, total dry weight, dry weight of the leaves, stems and roots, G value (total plant dry weight/seedling days), chlorophyll content, photosynthetic rate, leaf-level and whole plant-level water use efficiency and cumulative water consumption of tomato seedlings were increased with increasing proportion of NO<sub>3</sub><sup>-</sup> in nutrient solutions in the elevated CO<sub>2</sub> treatment. Plant biomass, plant height, stem thickness and photosynthetic rate were 67%, 22%, 24% and 55% higher at elevated CO<sub>2</sub> concentration than at ambient CO<sub>2</sub> concentration, depending on the values of NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratio. These results indicated that elevating CO<sub>2</sub> concentration did not mitigate the adverse effects of 100% NH<sub>4</sub><sup>+</sup>-N (in nutrient solution) on the tomato seedlings. At both CO<sub>2</sub> levels, NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratios of nutrient solutions strongly influenced almost every measure of plant performance, and nitrate-fed plants attained a greater biomass production, as compared to ammonium-fed plants. These phenomena seem to be related to the coordinated regulation of photosynthetic rate and cumulative water consumption of tomato seedlings.

**Key words:** CO<sub>2</sub> enrichment; NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratio; physiological and biochemical indices; growth; water use; tomato seedling

### Introduction

It is well known that atmospheric CO<sub>2</sub> concentration increases as a consequence of human activities, e.g. increased fossil fuel burning associated with industrialization, increased cement production, and transformation of land use from agriculture to non-agriculture purposes. Recent research on the effects of the increased atmospheric CO<sub>2</sub> concentration on plants has been intensified (Allen, 1994; Asseng *et al.*, 2004; BassiriRad *et al.*, 1999; Gill *et al.*, 2002; Kimball, 1983; Poorter *et al.*, 1996; Van Vuuren *et al.*, 1997; Woodrow, 1994). Many researches demonstrated that, for many C<sub>3</sub> species, high atmospheric CO<sub>2</sub> concentration led to increases in photosynthetic rate, whole-plant growth, and water use efficiency (WUE). It also decreased stomatal conductance and transpiration rate (Kimball *et al.*, 2002; Rogers and Dahlman, 1993; Rogers *et al.*, 1999; Woodward *et al.*, 1991). The plant responses to a high CO<sub>2</sub> level are different, depending on their growth conditions and environmental factors such as tropospheric

ozone, temperature, water, irradiance, nitrogen and potassium nutrition levels (Bauer *et al.*, 2001; Ceulemans and Mousseau, 1994; Olszyk and Wise, 1997; Heaton *et al.*, 2004; Fangmeier *et al.*, 1999; Rawson, 1995; Silberbush *et al.*, 2003; Sionit *et al.*, 1982; Torbert *et al.*, 2004). However, little information about interactive effects of CO<sub>2</sub> and nitrogen is available. Cruz *et al.* (1997) indicated that the response of carob to high CO<sub>2</sub> concentrations was very much dependent on nitrogen source, the morphology of root systems of nitrate-fed plants changed in the presence of elevated CO<sub>2</sub> concentrations, resembling, more closely, that of ammonium-fed plants. Total leaf area was higher in ammonium- than in nitrate-fed plants. Elevated CO<sub>2</sub> increases the growth of *Betula alleghaniensis*, significantly, regardless of the source of N. However it showed no significant difference in biomass production and allocation on *Pinus strobus*, and both species exhibited significantly greater growth with NH<sub>4</sub><sup>+</sup> than with NO<sub>3</sub><sup>-</sup>, along with lower root: shoot biomass ratios (Bauer and Berntson, 2001). Causin *et al.* (2004) pointed out that a high NO<sub>3</sub><sup>-</sup>:NH<sub>4</sub><sup>+</sup> ratio stimulated growth responses to elevated CO<sub>2</sub> in *Prosopis glandulosa* and *Prosopis flexuosa*. Therefore, it is necessary to understand plant growth responses to various

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ratios of NO<sub>3</sub><sup>-</sup>:NH<sub>4</sub><sup>+</sup> and at elevated CO<sub>2</sub> condition.

Tomato is an important vegetable, and there have been many studies on how elevated CO<sub>2</sub> affects the biochemical or physiological processes of tomato as well as the quality and productivity of tomato (Bertin and Gary, 1998; Islam *et al.*, 1996; Madsen, 1974; Morgan, 1971; van Oosten and Besford, 1995). The studies on interactive effects of elevated CO<sub>2</sub> concentration and the growth on tomato have focused on tropospheric ozone, water, irradiance, ultraviolet-B, salt and CO<sub>2</sub> enrichment (Maggio *et al.*, 2002; Morgan, 1971; Newton, 1966; Olszyk and Wise, 1997; Paez *et al.*, 1984; Yu *et al.*, 2004). However, the interactive effects of CO<sub>2</sub> and different NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratios on tomato seedling have not been studied. In this study, we investigated the effect of CO<sub>2</sub> enrichment on the growth, morphology, chlorophyll content and water use of tomato seedlings, which were grown in nutrient solutions with different NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratios. The information from this study can be useful to facilitate fertilizer management of this important crop, especially under the condition of increasingly enhanced CO<sub>2</sub> concentration.

## 1 Materials and methods

### 1.1 Plant materials and growth conditions

Tomato (*Lycopersicon esculentum* Mill. var. Hezuo 906) seeds were first sterilized in 10% (m/v) Na<sub>3</sub>PO<sub>4</sub> solution for 25 min, and thoroughly washed with distilled water. These seeds were germinated on a moistened filter paper at 25°C in the dark for 3 d, and sown in wet coarse sand. Tomato seedlings were selected for uniformity after the first true leaf emerged, and transplanted to a 1.2-L polypropylene container with different N (nitrate/ammonium concentration percentages of 100:0, 75:25, 50:50, 25:75, 0:100) nutrient solutions, respectively. The nutrient solutions also contained: 25 μmol/L FeNa-EDTA, 23 μmol/L H<sub>3</sub>BO<sub>3</sub>, 4.8 μmol/L MnSO<sub>4</sub>·4H<sub>2</sub>O, 3.8 μmol/L ZnSO<sub>4</sub>·7H<sub>2</sub>O, 0.16 μmol/L CuSO<sub>4</sub>·5H<sub>2</sub>O and 0.01 μmol/L (NH<sub>4</sub>)<sub>6</sub>Mo<sub>7</sub>O<sub>24</sub>·H<sub>2</sub>O, and other components as shown in Table 1. The plants were fixed in a polypropylene cavity with a sponge, and grew in CO<sub>2</sub> growth chambers with ambient (360 μl/L) and elevated (720 μl/L) CO<sub>2</sub>, respectively. Each pot contained 2 seedlings. The growth chambers we controlled with 65% relative humidity and a photosynthetic photon flux of 600 μmol/(m<sup>2</sup>·s) and

a photoperiod of 14 h at 25°C/15°C (day/night) at air temperature. The dispensing of CO<sub>2</sub> in the CO<sub>2</sub> growth chambers started on day 1 after the transplanting, and the CO<sub>2</sub> levels were maintained 24 h/d until the final harvest. All nutrient solutions were prepared with deionized water. After an initial growth period of 7 d, nutrient solutions were refreshed every 4 d. The pH of the solution was adjusted to 6.0±0.2 with dilute NaOH or HCl. All treatments were replicated 3 times using a full-factorial design.

Forty-five days after the transplanting, tomato seedlings were harvested and divided into leaves, stems and roots. The number of leaves and flower per plant were recorded before the harvest. Roots were rapidly washed in distilled water, and all samples were weighted and dried immediately in an air-forced oven at 75°C to constant weight.

### 1.2 Leaf physiological indices measurement and chlorophyll content measurement

Forty-three days after the transplanting, newly fully expanded leaves (the third leaf from the top) were selected to determine leaf chlorophyll level. Leaf photosynthetic rate, transpiration rate and stomatal conductance were measured with a portable photosynthesis system (LI-6400, Li-Cor, Lincoln, NE, USA). The leaf segments were then homogenized using a mortar and pestle in 80% (v/v) acetone, and centrifuged for 15 min at 23000×g. Chlorophyll content was determined spectrophotometrically in the clear supernatant by measuring the absorbance at 665 and 643 nm in corresponding to chlorophyll *a* and *b*. The measurements were calculated into chlorophyll *a* or *b* according to Arnon (1949).

### 1.3 Water use

During the experiment, weigh the weight of container before and after culture and the lost weight regarded as water consumption. Cumulative water consumption per plant (CWC<sub>p</sub>) was calculated from the sum of water consumption per tomato seedling. In order to distinguish WUE at the leaf and for whole plant, water use efficiency of photosynthesis (WUE<sub>L</sub>, calculated as photosynthetic rate/transpiration rate) and water use efficiency of productivity (WUE<sub>p</sub>, from the total dry weight per plant at harvest divided by cumulative water consumption per plant) were analyzed. WUE<sub>L</sub> and WUE<sub>p</sub> was measured for 45-d-old plants.

### 1.4 Parameter calculation and statistical analysis

The growing value (*G* value) was calculated as: (total plant dry weight)/(seedling days). Variance analysis was used, and the means were separated by Duncan's multiple range test (DMRT) at 5% level. Analysis of variance (ANOVA) was performed using the general linear model-univariate procedure from SPSS software. The ANOVA tests were done with CO<sub>2</sub> and NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratio as the main effects, including two-way interactions.

## 2 Results

### 2.1 Effect on chlorophyll content and physiological indices of tomato seedlings

**Table 1 Nutrient solution composition (μmol/L) at a constant N concentration (3.835 mmol/L) and different NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratios**

Nutrient source	NH <sub>4</sub> <sup>+</sup> :NO <sub>3</sub> <sup>-</sup>				
	0/100	25/75	50/50	75/25	100/0
Ca(NO <sub>3</sub> ) <sub>2</sub>	1085	750	750	480	0
NH <sub>4</sub> NO <sub>3</sub>	0	624	418	0	0
KNO <sub>3</sub>	1665	753	0	0	0
(NH <sub>4</sub> ) <sub>2</sub> SO <sub>4</sub>	0	0	582	1270	1750
NH <sub>4</sub> H <sub>2</sub> PO <sub>4</sub>	0	335	335	335	335
KH <sub>2</sub> PO <sub>4</sub>	335	0	0	0	0
K <sub>2</sub> SO <sub>4</sub>	0	624	1000	1000	1000
MgSO <sub>4</sub>	500	500	500	500	500
CaCl <sub>2</sub>	0	0	0	270	750

Different ratios of  $\text{NH}_4^+/\text{NO}_3^-$  significantly affected chlorophyll content of tomato leaves in that total chlorophyll content and chlorophyll *a* and *b* contents were all depressed when  $\text{NH}_4\text{-N}$  was the only source of N (Table 2).

Photosynthetic rate, transpiration rate and stomatal conductance were all significantly influenced by the solution  $\text{NH}_4^+/\text{NO}_3^-$  ratio and  $\text{CO}_2$  concentration as well as the interactions of  $\text{NH}_4^+:\text{NO}_3^-$  ratio and  $\text{CO}_2$  (Table 3). The photosynthetic rate of tomato leaves in the elevated  $\text{CO}_2$  treatment was significantly higher than those in the ambient  $\text{CO}_2$  treatment at their comparable  $\text{NH}_4^+:\text{NO}_3^-$  ratios, except for 100%  $\text{NH}_4\text{-N}$  in the nutrient solution. At the same solution  $\text{NH}_4^+/\text{NO}_3^-$  ratio, transpiration rate and stomatal conductance were significantly lower with elevated  $\text{CO}_2$  concentration than the ambient  $\text{CO}_2$  concentration. At both  $\text{CO}_2$  levels, photosynthetic rate, transpiration rate and stomatal conductance of the plants increased with increasing proportion of  $\text{NO}_3^-$  in the nutrient solutions.

## 2.2 Effects on the growth of tomato seedlings

Total plant dry weight, the dry weight of roots, leaves and stems, and the root/shoot ratio were all significantly influenced by  $\text{NH}_4^+/\text{NO}_3^-$  ratios and  $\text{CO}_2$  levels as well as the interactions of  $\text{NH}_4^+:\text{NO}_3^-$  and  $\text{CO}_2$  (Table 4). For the elevated  $\text{CO}_2$ , the dry weight of the total plant biomass, leaves and stems increased by -5%–67%, -12%–75% and -4%–44%, respectively. The dry weight of roots increased by -40%–78% compared to the ambient  $\text{CO}_2$  level. The dry weight of total plant biomass, roots, leaves and stems increased as  $\text{NO}_3^-$  proportion increases in the nutrient solutions at both  $\text{CO}_2$  levels. Little effect of  $\text{CO}_2$  on the root/shoot ratio was observed, however, they appeared to be an increase trend with increasing proportion of  $\text{NH}_4$  in the culture solution. The increase in dry weight of the total plant biomass and stems and leaves with decreasing solution  $\text{NH}_4^+/\text{NO}_3^-$  ratio was greater at the elevated  $\text{CO}_2$  concentration than at the ambient  $\text{CO}_2$  concentration. However, root dry weight was little affected by  $\text{NH}_4^+/\text{NO}_3^-$  ratio at the ambient  $\text{CO}_2$  concentration, and it was higher at the elevated  $\text{CO}_2$  concentration with

**Table 2 Effect of  $\text{CO}_2$  on leaf chlorophyll content of tomato seedlings grown in nutrient solutions with different  $\text{NH}_4^+/\text{NO}_3^-$  ratios**

$\text{CO}_2$ concentration ( $\mu\text{L/L}$ )	$\text{NH}_4^+/\text{NO}_3^-$	Chl- <i>a</i> (mg/g fresh weight)	Chl- <i>b</i> (mg/g fresh weight)	Total Chl (mg/g fresh weight)
720	0/100	1.11±0.16 a	0.60±0.08 ab	1.70±0.24 a
	25/75	1.03±0.11 ab	0.61±0.07 ab	1.64±0.18 a
	50/50	1.12±0.30 a	0.62±0.09 ab	1.73±0.40 a
	75/25	1.27±0.21 a	0.66±0.08 ab	1.92±0.29 a
	100/0	0.46±0.19 c	0.20±0.04 c	0.66±0.24 b
360	0/100	0.95±0.15 ab	0.53±0.11 b	1.49±0.26 a
	25/75	1.00±0.17 ab	0.54±0.12 b	1.54±0.29 a
	50/50	1.09±0.14 a	0.60±0.08 ab	1.69±0.21 a
	75/25	1.25±0.12 a	0.71±0.05 a	1.96±0.17 a
	100/0	0.70±0.19 bc	0.27±0.06 c	0.98±0.24 b
Analysis of variance				
		Chl- <i>a</i>	Chl- <i>b</i>	Total Chl
	$\text{NH}_4^+:\text{NO}_3^-$ ratio	***	***	***
	$\text{CO}_2$	ns	ns	ns
	$\text{NH}_4^+:\text{NO}_3^-$ ratio × $\text{CO}_2$	ns	ns	ns

Means within a column followed by the same letter(s) are not significantly different at  $P > 0.05$  based on Duncan's Multiple Range Test. Data represent means ± standard deviation.  $P$ -value indicates significance level based on two-way ANOVA. \*\*\* $P < 0.001$ ; ns, not significant.

**Table 3 Effects of  $\text{CO}_2$  on photosynthesis and transpiration of leaves of tomato seedlings grown in nutrient solutions with different  $\text{NH}_4^+/\text{NO}_3^-$  ratios**

$\text{CO}_2$ concentration ( $\mu\text{L/L}$ )	$\text{NH}_4^+/\text{NO}_3^-$	Photosynthetic rate ( $\mu\text{mol CO}_2/(\text{m}^2 \cdot \text{s})$ )	Transpiration rate ( $\text{mmol H}_2\text{O}/(\text{m}^2 \cdot \text{s})$ )	Stomatal conductance ( $\text{mmol H}_2\text{O}/(\text{m}^2 \cdot \text{s})$ )
720	0/100	26.6±1.0 a	2.72±0.04 bc	0.121±0.005 cd
	25/75	23.0±0.7 b	2.48±0.05 d	0.118±0.007 d
	50/50	19.8±1.0 c	2.28±0.16 e	0.106±0.007 e
	75/25	11.6±1.0 g	2.05±0.07 f	0.097±0.010 e
	100/0	4.7±0.7 i	1.52±0.11 g	0.069±0.007 f
360	0/100	17.2±0.7 d	3.31±0.08 a	0.157±0.004 a
	25/75	15.5±1.1 e	3.22±0.05 a	0.137±0.005 b
	50/50	13.0±0.2 f	2.85±0.10 b	0.131±0.003 bc
	75/25	9.9±0.4 h	2.66±0.06 c	0.122±0.006 cd
	100/0	5.9±0.2 i	2.33±0.09 de	0.120±0.006 cd
Analysis of variance				
		Photosynthetic rate	Transpiration rate	Stomatal conductance
	$\text{NH}_4^+:\text{NO}_3^-$ ratio	***	***	***
	$\text{CO}_2$	***	***	***
	$\text{NH}_4^+:\text{NO}_3^-$ ratio × $\text{CO}_2$	***	***	***

Means within a column followed by the same letter(s) are not significantly different at  $P > 0.05$  based on Duncan's Multiple Range Test. Data represent means ± standard deviation.  $P$ -value indicates significance level based on two-way ANOVA. \*\*\* $P < 0.001$ .

**Table 4 Effect of CO<sub>2</sub> on the dry weight and the ratio of dry weight of root to shoot of the tomato seedlings grown in nutrient solutions with different NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratios**

CO <sub>2</sub> concentration (μL/L)	NH <sub>4</sub> <sup>+</sup> /NO <sub>3</sub> <sup>-</sup>	Total plant (g/plant)	Root (g/plant)	Leaf (g/plant)	Stem (g/plant)	Dry weight of root/shoot
720	0/100	6.02±0.16 a	0.57±0.04 a	4.03±0.08 a	1.41±0.06 a	0.10±0.00 e
	25/75	4.24±0.03 b	0.45±0.01 b	2.76±0.01 b	1.03±0.01 b	0.12±0.00 de
	50/50	2.92±0.17 e	0.42±0.03 b	1.68±0.12 e	0.82±0.02 c	0.17±0.00 b
	75/25	2.01±0.12 f	0.24±0.04 d	1.27±0.06 f	0.50±0.03 e	0.14±0.02 cd
	100/0	0.44±0.01 g	0.06±0.00 e	0.30±0.01 h	0.08±0.00 f	0.17±0.01 b
360	0/100	3.60±0.32 c	0.32±0.03 c	2.31±0.19 c	0.98±0.10 b	0.10±0.00 e
	25/75	3.29±0.03 d	0.41±0.03 b	2.15±0.01 d	0.73±0.01 d	0.14±0.01 cd
	50/50	2.91±0.02 e	0.40±0.01 b	1.80±0.05 e	0.71±0.04 d	0.16±0.00 bc
	75/25	1.86±0.04 f	0.40±0.05 b	0.94±0.01 g	0.52±0.00 e	0.28±0.04 a
	100/0	0.46±0.02 g	0.06±0.00 e	0.34±0.02 h	0.06±0.00 f	0.16±0.01 bc
Analysis of variance		Total plant	Root	Leaf	Stem	Root/shoot
NH <sub>4</sub> <sup>+</sup> :NO <sub>3</sub> <sup>-</sup> ratio		***	***	***	***	***
CO <sub>2</sub>		***	***	***	***	***
NH <sub>4</sub> <sup>+</sup> :NO <sub>3</sub> <sup>-</sup> ratio × CO <sub>2</sub>		***	***	***	***	***

Means within a column followed by the same letter(s) are not significantly different at  $P > 0.05$  based on Duncan's Multiple Range Test. Data represent means ± standard deviation.  $P$ -value indicates significance level based on two-way ANOVA. \*\*\* $P < 0.001$ .

decreasing NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratio. This suggests that the effect of NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratio on the growth of tomato seedlings is greater at the elevated CO<sub>2</sub> concentration than at the ambient CO<sub>2</sub> concentration, and dry matter seems to be preferentially allocated to roots when a high NO<sub>3</sub><sup>-</sup> proportion is supplied. The number of buds and blossoms of tomato seedlings increased with increasing proportion of NO<sub>3</sub><sup>-</sup> in nutrient solution (data not shown).

The effects of NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratio and CO<sub>2</sub> concentration as well as the interactions of NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratio and CO<sub>2</sub> on the  $G$  value, stem thickness, stem length and root length (Table 5) are significant. Compared to the ambient CO<sub>2</sub> concentration  $G$  value, stem thickness and stem length of the plants were 67%, 24%, and 22% higher than those at the elevated CO<sub>2</sub> concentration. Those values were greater under the elevated CO<sub>2</sub> concentration than those under the ambient CO<sub>2</sub> concentration if a high proportion of NO<sub>3</sub><sup>-</sup> is supplied. Root length was reduced when only as NH<sub>4</sub><sup>+</sup>-N was supplied. These results indicated that tomato seedling growth was promoted under elevated CO<sub>2</sub> concentration when a high NO<sub>3</sub><sup>-</sup> proportion of N was supplied, but the

benefit of the elevated CO<sub>2</sub> did not surpass the adverse effect of having all N in the form of NH<sub>4</sub><sup>+</sup>-N.

### 2.3 Effects on water use of tomato seedlings

The effects of NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratio and CO<sub>2</sub> level as well as the interactions of NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratio and CO<sub>2</sub> on WUE<sub>p</sub> and WUE<sub>L</sub> were also significant, and the effects of NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratio and the interactions of NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratio and CO<sub>2</sub> on CWC<sub>p</sub> were significant, although CO<sub>2</sub> had no impact on CWC<sub>p</sub> (Fig.1).

Cumulative water consumption of tomato seedlings (CWC<sub>p</sub>) was slightly higher at the elevated CO<sub>2</sub> concentration than the ambient CO<sub>2</sub> concentration when high proportions of NO<sub>3</sub><sup>-</sup> were supplied. It was significantly low when NH<sub>4</sub><sup>+</sup>:NO<sub>3</sub><sup>-</sup> ratio was 50/50, and slightly lower when high proportions of NH<sub>4</sub><sup>+</sup> were supplied.

Whole plant-level water use efficiency (WUE<sub>p</sub>) decreased with increasing proportion of NH<sub>4</sub><sup>+</sup>-N as N source and this effect was greater at the elevated CO<sub>2</sub> concentration than the ambient CO<sub>2</sub> concentration. The positive trend of the combined elevated CO<sub>2</sub> and NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratio

**Table 5 Effect of CO<sub>2</sub> on morphological indices of tomato seedlings grown in nutrient solutions with different NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratios**

CO <sub>2</sub> concentration (μL/L)	NH <sub>4</sub> <sup>+</sup> /NO <sub>3</sub> <sup>-</sup>	$G$ value (g/d)	Stem thickness (mm)	Stem length (mm)	Root length (mm)
720	0/100	0.13±0.00 a	7.4±0.04 a	290±1.58 a	253±1.30 bc
	25/75	0.09±0.00 b	6.2±0.01 b	265±0.97 b	228±0.63 d
	50/50	0.06±0.00 e	6.1±0.02 bc	217±0.33 d	233±0.78 d
	75/25	0.04±0.00 f	5.6±0.03 bc	194±0.36 e	259±0.35 ab
	100/0	0.01±0.00 g	3.5±0.02 d	65±0.42 g	170±1.21 e
360	0/100	0.08±0.01 c	6.0±0.01 bc	243±0.37 c	239±0.77 cd
	25/75	0.07±0.00 d	6.1±0.02 bc	232±0.91 cd	254±0.94 bc
	50/50	0.06±0.00 e	5.6±0.03 c	218±2.16 d	270±0.72 a
	75/25	0.04±0.00 f	5.5±0.08 c	159±2.26 f	273±0.35 a
	100/0	0.01±0.00 g	3.4±0.00 d	63±0.28 g	170±0.12 e
Analysis of variance		$G$ value	Stem thickness	Stem length	Root length
NH <sub>4</sub> <sup>+</sup> :NO <sub>3</sub> <sup>-</sup> ratio		***	***	***	***
CO <sub>2</sub>		***	***	***	***
NH <sub>4</sub> <sup>+</sup> :NO <sub>3</sub> <sup>-</sup> ratio × CO <sub>2</sub>		***	***	***	***

Means within a column followed by the same letter(s) are not significantly different at  $P > 0.05$  based on Duncan's Multiple Range Test. Data represent means ± standard deviation.  $P$ -value indicates significance level based on two-way ANOVA. \*\*\* $P < 0.001$ .

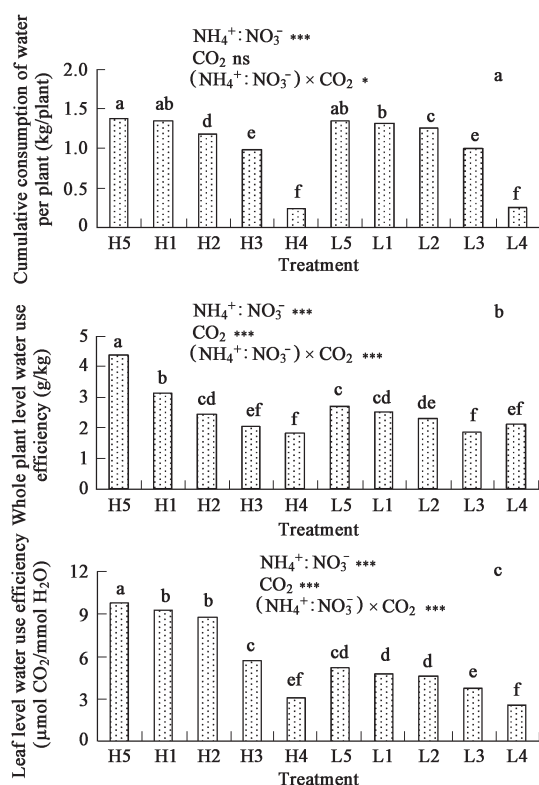


Fig. 1 Effect of CO<sub>2</sub> on water use of tomato seedlings in nutrient solution with different NH<sub>4</sub><sup>+</sup>:NO<sub>3</sub><sup>-</sup> ratios. H: CO<sub>2</sub> concentration; L: ambient CO<sub>2</sub> concentration; 5, 1, 2, 3, 4 represent 0/100, 25/75, 50/50, 75/25, 100/0 of NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratio in nutrient solution. (a) cumulative consumption of water per plant (CWC<sub>p</sub>); (b) whole plant-level water use efficiency (WUE<sub>p</sub>); (c) leaf-level water use efficiency (WUE<sub>L</sub>). Bars with the same letter are not significantly different at  $P > 0.05$  by Duncan's multiple range test. Significance levels from ANOVA for CO<sub>2</sub>, NH<sub>4</sub><sup>+</sup>:NO<sub>3</sub><sup>-</sup>, (NH<sub>4</sub><sup>+</sup>:NO<sub>3</sub><sup>-</sup>) × CO<sub>2</sub>; (\*\*\*), (\*\*), (\*), ns for  $P \leq 0.001$ ,  $P \leq 0.01$ ,  $P \leq 0.05$ , and not significant, respectively. Data points are the mean of three replicates for each treatment.

on WUE<sub>p</sub> was the result of a greater DM production rather than decreasing water consumption.

Leaf-level water use efficiency (WUE<sub>L</sub>) in the CO<sub>2</sub> enriched treatment was significantly higher than those in the ambient CO<sub>2</sub> treatment at comparable NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratios, except for 100% NH<sub>4</sub><sup>+</sup>-N nutrient solution. At both CO<sub>2</sub> levels, WUE<sub>L</sub> increased as increasing proportion of NO<sub>3</sub><sup>-</sup> in the nutrient solutions. This positive effect of elevated CO<sub>2</sub> on WUE<sub>L</sub> was due to reductions in leaf conductance, and, when it was combined with NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratios, this phenomenon was linked to the increased photosynthesis (Table 3).

## 3 Discussion

### 3.1 Photosynthesis

The results from this study are consistent with many other studies (Wand *et al.*, 1999; Das *et al.*, 2000). Greater photosynthesis rates at high NO<sub>3</sub><sup>-</sup> concentration appear to be driven by changes in plant-water relations. In this regard, our results are consistent with other studies, in which decreased stomatal conductance and water uptake under NH<sub>4</sub><sup>+</sup> nutrition were reported in a variety of plant species

(Adler *et al.*, 1996; Guo *et al.*, 2002; Lu *et al.*, 2005; Pill and Lambeth, 1977). The increased root:shoot ratio under high proportion of NH<sub>4</sub><sup>+</sup> in nutrition may play a role in the decrease of stomatal conductance; however, it has also been implicated that decreased root hydraulic conductivity (Adler *et al.*, 1996; Guo *et al.*, 2002) and elevated abscisic acid levels under NH<sub>4</sub><sup>+</sup> nutrition might also contribute to this phenomenon (Jeschke and Hartung, 2000; Peuke *et al.*, 1994). Regardless of the mechanism, it is clear that photosynthetic performance of tomato seedlings declined markedly under high NH<sub>4</sub><sup>+</sup> proportion in relative to high NO<sub>3</sub><sup>-</sup> proportion.

### 3.2 Leaf chlorophyll content

Elevated CO<sub>2</sub> concentration did not affect leaf chlorophyll *a* and *b* as well as total chlorophyll concentration of tomato leaves. Similarly, chlorophyll content in soybean increased in mature leaves after they were exposed to high CO<sub>2</sub> concentration (Allen *et al.*, 1988; Vu *et al.*, 2001). However, chlorophyll in young leaves (3 week old soybean plants) was not affected by elevated CO<sub>2</sub> (Sicher *et al.*, 1995). Decreases in leaf chlorophyll under an elevated CO<sub>2</sub> concentration have also been reported by DeLucia *et al.* (1985) and Radoglou and Jarvis (1992). At both CO<sub>2</sub> levels in this study, NH<sub>4</sub><sup>+</sup> as the sole source of N significantly decreased tomato leaf chlorophyll content, indicating a possible toxic effect. The possible leaf toxicity symptoms (chlorosis and diminution of chlorophyll content) in the 100% NH<sub>4</sub><sup>+</sup>-N solution may have been resulted from chloroplastic membrane structure destabilization that was due to peroxidation of their lipid constituents, a phenomenon confirmed by Tan *et al.* (2000).

### 3.3 Plant growth

The results showed that the increase of tomato seedling growth and biomass accumulation due to the decrease of NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratio in nutrient solutions was greater with the elevated CO<sub>2</sub> concentration than with the ambient CO<sub>2</sub> concentration. Growth inhibition by a high NH<sub>4</sub><sup>+</sup> proportion may be due to the toxicity of NH<sub>4</sub><sup>+</sup> because browning of leaf margin, partial leaf yellowing, mottled chlorosis, and curing and brown roots were observed in the plants with the treatment of the highest proportion of NH<sub>4</sub><sup>+</sup>-N. Many studies have shown reduced root growth with NH<sub>4</sub><sup>+</sup> as the sole source of N (Cramer and Lewis, 1993; Findenegg, 1987). Several hypotheses have been proposed to explain this: (1) a direct toxicity of a high intracellular NH<sub>4</sub><sup>+</sup> content (Mehrer and Mohr, 1989), (2) a decrease in the pH of the rhizosphere associated with the uptake and assimilation of NH<sub>4</sub><sup>+</sup> (Findenegg, 1987), and (3) competition for saccharides as related to the assimilation of NH<sub>4</sub><sup>+</sup> by roots (Cramer and Lewis, 1993). Therefore, we suggest that the suppression of root growth at high NH<sub>4</sub><sup>+</sup>:NO<sub>3</sub><sup>-</sup> ratios may have been a dominant factor, and therefore, under elevated atmospheric CO<sub>2</sub>, the growth of tomato seedlings benefits only when NO<sub>3</sub><sup>-</sup> is the main N source.

On the other hand, Bloom *et al.* (2002) found that when wheat plants received NO<sub>3</sub><sup>-</sup> rather than NH<sub>4</sub><sup>+</sup> as

the nitrogen source, CO<sub>2</sub> enrichment of shoot growth was halved and CO<sub>2</sub> inhibition of shoot protein was doubled. Heeb *et al.* (2005a) found that ammonium is an equivalent nitrogen source for tomato plants compared with nitrate. They also found that tomato fruit quality was actually higher in NH<sub>4</sub><sup>+</sup> fertilized plants compared to those provided NO<sub>3</sub><sup>-</sup>. In a related study, no significant differences in shoot biomass and yields of red tomatoes were observed between NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup>-fed plants (Heeb *et al.*, 2005b). These discrepancies may be due to difference of the crops and the differences in growth conditions and sampling.

### 3.4 Partitioning of biomass

The growth responses of individual organs to a particular treatment did not follow the same pattern as for the whole plant. At high NH<sub>4</sub><sup>+</sup> proportions, dry matter appeared to be preferentially allocated to roots, indicating that tomato seedlings adapted to the stress from NH<sub>4</sub><sup>+</sup> toxicity by adjusting resources internally. Optimal partitioning models and its theory suggest that plants respond to variation in the environment by partitioning dry weight among plant organs to optimize the capture of resources to maximize plant growth rate (Brouwer, 1983; McConnaughay and Coleman, 1999; Reynolds and Thornley, 1982; Wilson, 1988).

### 3.5 Water use

This study is in agreement with previous studies, which showed that atmospheric CO<sub>2</sub> enrichment increases cumulative water consumption and water use efficiency, and reduces stomatal conductance and transpiration rate (Bowler and Press, 1996; Centritto *et al.*, 2002; Kimball *et al.*, 2002; Rogers and Dahlman, 1993; Rogers *et al.*, 1999; Woodward *et al.*, 1991). The decrease in stomatal conductance reduced transpiration per unit leaf area (Drake and Gonzalez-Meler, 1997; Kimball *et al.*, 2002). However, several feedbacks tend to diminish the effect of reduced conductance in terms of its effects on canopy evapotranspiration (Jarvis and McNaughton, 1986). A major counterbalancing effect arises when leaf area per plant increases due to elevated CO<sub>2</sub> concentrations. No savings in water use can be expected in canopies where elevated CO<sub>2</sub> stimulates an increase in leaf area that offsets the decrease in stomatal conductance. Stomatally-reduced transpiration rate has been observed to counter-balance increased leaf area in C<sub>3</sub> plants, such that water use per plant was similar for the control and CO<sub>2</sub>-enriched plants (Chaudhuri *et al.*, 1990; Hunsaker *et al.*, 1994, 1996, 2000; Kimball and Idso, 1983). In agreement with most previous reports (Adler *et al.*, 1996; Guo *et al.*, 2002), our results showed that, at both CO<sub>2</sub> levels, the stomatal conductance decreased to a greater extent in the high NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratio treatments than in the low NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratio treatment.

Our results also indicated that WUE may also be altered by both CO<sub>2</sub> and NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratios. WUE<sub>L</sub> are very sensitive to rising CO<sub>2</sub>. The great photosynthetic water use efficiency (WUE<sub>L</sub>) of plants grown at the elevated CO<sub>2</sub> was associated with the reduced stomatal conductance, and, when it was combined with lower NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratio, this

stimulation was linked to the increased photosynthesis. In our study, WUE<sub>p</sub>, like WUE<sub>L</sub>, was also positively affected by the elevated CO<sub>2</sub>, although the response was limited to the plants grown at high NH<sub>4</sub><sup>+</sup> proportion. Interaction of the elevated CO<sub>2</sub> and high proportion of NO<sub>3</sub><sup>-</sup>-N enhanced WUE<sub>p</sub>, as a result of great dry matter production in the plants grown at the elevated CO<sub>2</sub> with high proportion of NO<sub>3</sub><sup>-</sup>-N supplied.

## 4 Conclusions

Elevated CO<sub>2</sub> has been proven to be beneficial for the growth of tomato seedlings (Madsen, 1974; Morgan, 1971). Our results confirmed the previous findings, and enhanced our understanding of underlying physiological processes, which can be helpful to improve the N fertilizer management of tomato seedlings in the future, especially in CO<sub>2</sub>-rich environment. Our results indicated that: (1) the effect of elevated CO<sub>2</sub> on the development and growth of tomato seedlings depended on NH<sub>4</sub><sup>+</sup>/NO<sub>3</sub><sup>-</sup> ratios. When applied at high NH<sub>4</sub><sup>+</sup> proportions, no effect of CO<sub>2</sub> was observed, whereas, at high proportion of NO<sub>3</sub><sup>-</sup>-N, biomass production was enhanced, as a result of stimulated photosynthetic rates and water use efficiency; (2) tomato seedling may benefit more from CO<sub>2</sub> enrichment when N nutrient is supplied at a high NO<sub>3</sub><sup>-</sup>-N proportion.

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