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RESEARCH ARTICLE

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Effect of interactions between carbon dioxide enrichment and NH_4^+/NO_3^- ratio on pH of culturing nutrient solution, growth and vigor of tomato root system

Abstract A growth chamber experiment was conducted to investigate the influence of NH_4^+/NO_3^- ratio and elevated CO_2 concentration on the pH in nutrient solution, growth and root vigor system of tomato seedling roots, which attempts to understand whether the elevated CO_2 concentration can alleviate the harmful effects of higher NH_4^+–N concentration in nutrient solutions on the tomato root system. Tomato (*Lycopersicon esculentum* Mill. var. Hezuo 906) was grown in pots with nutrient solutions varying in NH_4^+/NO_3^- ratio (0:1, 1:3, 1:1, 3:1 and 1:0) and the growth chambers were supplied with ambient (360 $\mu L \cdot L^{-1}$) or elevated CO_2 concentration (720 $\mu L \cdot L^{-1}$). The results showed that the pH changed with the growth process and CO_2 concentration increased. At both CO_2 levels, pH increased when 100% NO_3^-–N was supplied and decreased in other treatments. The pH decrease in the nutrient solution was directly correlated to the NH_4^+-N proportion. The pH value was more reduced in 100% NH_4^+–N nutrient solution than increased in the 100% NO_3^-–N nutrient solution. CO_2 enrichment increased the dry weight of shoots and roots, root vigor system, total absorbing area and active absorbing area of tomato seedlings. All the measurement indexes above were increased in the elevated CO_2 concentration treatment with the NO_3^- proportion increase in the nutrient solutions. Thus, under the elevated CO_2 concentration, the dry weights of shoots and roots, root vigor system, total root absorbing area and active absorbing area were found to be inversely correlated to NH_4^+/NO_3^- ratio, leading to about 65.8%, 78.0%, 18.9%, 12.9% and 18.9% increase, respectively, compared with that under the ambient CO_2 concentration. Our results indicated that tomato seedling roots may benefit mostly from CO_2 enrichment when 100% NO_3^-–N nutrient solutions was supplied, but the CO_2 concentration elevation did not alleviate the harmful effects when 100% NH_4^+–N was supplied.

Keywords tomato, pH, roots, growth and development

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1 Introduction

Tomato root is an important organ for nutrient uptake, thus the number and activity of its roots will have a great impact on the growth, development and morphological formation of the aboveground parts. Many studies have shown that elevated CO_2 concentration could promote root growth and increase root volume (Xu, 1994; Zhang et al., 1999; Li et al., 2005a). Wei et al. (2000) suggested that elevated CO_2 concentration could also enhance root vigor, total absorbing area and active absorbing area. However, there are some inverse results. Yang et al. (2006) found that elevated CO_2 concentration increased root volume, whereas it significantly reduced root vigor, total absorbing area, and active absorbing area. The elevated CO_2 concentration could increase the root-to-shoot ratio at higher concentration nutrient solution and reduce the ratio at a lower concentration (Li et al., 2005b). The above results indicate that with the variety of crops, growth conditions and environmental factors, the growth and development of roots can have different responses to CO_2 enrichment.

Root growth is inhibited when NH_4^+–N is the sole source of N (Cramer and Lewis, 1993; Findenegg, 1987). Several hypotheses have been proposed to explain this result: (1) a direct toxicity of a high intracellular NH_4^+–N content (Mehrer and Mohr, 1989); (2) a decrease in the pH of the rhizosphere associated with the uptake and assimilation of NH_4^+–N (Findenegg, 1987); and (3) competition for saccharides as related to the assimilation of NH_4^+–N by roots (Cramer and Lewis, 1993). Therefore, we can speculate that the high NH_4^+/NO_3^- ratio is probably considered as a dominant growth inhibition factor to the root growth. Does elevated CO_2 concentration alleviate the effect of NH_4^+–N on the root growth suppression? How far is it? This is an issue worth discussing. In our experiment, we investigated the effect of CO_2 enrichment and NH_4^+/NO_3^- ratio on the nutrient solution pH and the growth, development, physiological characteristics of tomato seedling roots. These results can enrich N theory, facilitate fertilizer management and also be helpful to produce healthy seedlings under elevated CO_2 concentration.

2 Materials and methods

2.1 Materials

Tomato (*Lycopersicon esculentum* Mill. var. Hezuo 906) is an early-medium maturing variety with strong disease resistance. Because of its big fruit, high yield, good commercial value, tolerance to high temperature, drought and shipment, it is cultivated widely throughout the tomato-producing areas in China.

2.2 Experimental design

Tomato seeds were first sterilized in 10% (m/v) Na_3PO_4 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 three days 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 $\mu mol \cdot L^{-1}$ FeNa-EDTA, 23 $\mu mol \cdot L^{-1}$ H_3BO_3, 4.8 $\mu mol \cdot L^{-1}$ $MnSO_4 \cdot 4H_2O$, 3.8 $\mu mol \cdot L^{-1}$ $ZnSO_4 \cdot 7H_2O$, 0.16 $\mu mol \cdot L^{-1}$ $CuSO_4 \cdot 5H_2O$ and 0.01 $\mu mol \cdot L^{-1}$ $(NH_4)_6MO_7O_{24} \cdot H_2O$, and other components as shown in Table 1. The plants were fixed in a polypropylene cavity with a sponge and grew in CO_2 growth chambers with ambient (360 $\mu L \cdot L^{-1}$) and elevated (720 $\mu L \cdot L^{-1}$) CO_2 concentrations, respectively. Each pot contained 2 seedlings. The growth chambers were controlled at a 65% relative humidity with a photosynthetic photon flux of 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and a photoperiod of 14 h at 25°C/15°C (day/night) air temperature. The dispensing of CO_2 in the CO_2 growth chambers started on Day 1 after the transplanting, and the CO_2 levels were maintained 24 h per day 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 diluted with NaOH or HCl. All treatments were replicated 3 times using a full-factorial design.

Table 1 The nutrient solution composition ($\mu mol \cdot L^{-1}$) at a constant N concentration (3.835 $mmol \cdot L^{-1}$) and different NH_4^+/NO_3^- ratios

nutrient source	NH_4^+(%)/NO_3^- (%)				
	0/100	25/75	50/50	75/25	100/0
$Ca(NO_3)_2$	1085	750	750	480	0
NH_4NO_3	0	624	418	0	0
KNO_3	1665	753	0	0	0
$(NH_4)_2SO_4$	0	0	582	1270	1750
$NH_4H_2PO_4$	0	335	335	335	335
KH_2PO_4	335	0	0	0	0
K_2SO_4	0	624	1000	1000	1000
$MgSO_4$	500	500	500	500	500
$CaCl_2$	0	0	0	270	750

Forty-five days after transplanting, tomato seedlings were harvested and divided into leaves, stems and roots. The roots were rapidly washed in distilled water and all samples were weighed and dried immediately in an air-forced oven at 75°C to the constant weight. The length of the longest root was determined using a plastic ruler.

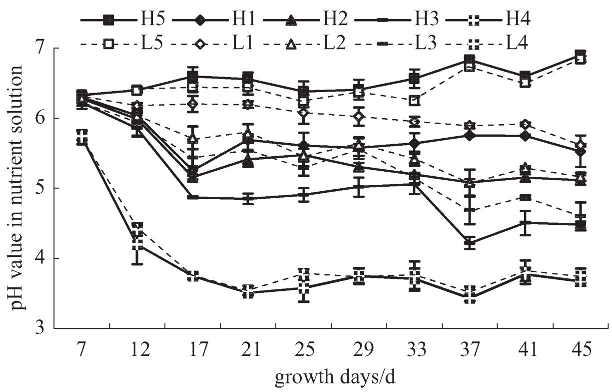

Fig. 1 Effect of CO_2 concentration on pH of nutrient solutions with different NH_4^+/NO_3^- ratios
Note: H represents elevated CO_2 concentration treatment; L represents ambient CO_2 treatment; 5, 1, 2, 3, 4 represent 0:1, 1:3, 1:1, 3:1, 1:0 of NH_4^+/NO_3^- ratio in nutrient solution, respectively. Vertical bars represent standard error, $n = 3$.

2.3 Root physiological indices measurement

Thirty-five days after transplanting, the root vigor system, total absorbing area and active absorbing area were measured. Root vigor was determined by the TTC method (Gao, 2000). Total absorbing area and active absorbing area were determined by the Methylene Blue method (Faculty of Plant Physiology, Department of Biology, East China Normal University, 1988).

2.4 Statistical analysis

Variance analysis was applied 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_2 and NH_4^+/NO_3^- ratio as the main effects, including two-way interactions.

3 Results

3.1 Effect of CO_2 concentration on nutrient solution pH with different NH_4^+/NO_3^- ratios

The nutrient solution pH values were measured after each culture (Fig. 1). The nutrient solution pH changed little after the first culture, but increased with the growth process and CO_2 enrichment. At both CO_2 levels, the nutrient solution pH increased when 100% NO_3^-–N was supplied, whereas it decreased to a different extent in other treatments. According to the charge balance principle, the nutrient solution pH would increase associating with HCO_3^- and OH^- releasing by the plant's uptake of NO_3^-–N and decrease associating with H^+ release by the uptake of NH_4^+–N. The pH value increased when the proportion of NO_3^-–N in the nutrient solutions was increased. The pH value increased to 6.90 and 6.84, respectively, in elevated and ambient CO_2 concentration, with 100% NO_3^-–N nutrient solution, whereas it decreased to 3.43 and 3.53, respectively, with 100% NH_4^+–N nutrient solution, compared with the control (6.0 ± 0.2).

3.2 Effect of CO_2 concentration on the growth and development of tomato seedling roots with different NH_4^+/NO_3^- ratios

The results showed that CO_2 concentration and NH_4^+/NO_3^- ratio, as well as the interactions of CO_2 and NH_4^+/NO_3^- ratio, had significant effects on the dry weights of roots, shoots, root to shoot ratio and root length (Table 2). CO_2 enrichment increased the dry weights of roots and shoots and root length at low NH_4^+/NO_3^- ratios and decreased the dry weights of roots and root length at high NH_4^+/NO_3^- ratios. Nevertheless, 100% NH_4^+–N nutrient solution conferred no impact on all the growth indices above. To the utmost extent, under the elevated CO_2 concentration, the dry weights of roots and shoots and root length increased by 78.0%, 65.8% and 5.9%, respectively, compared with that under the ambient concentration. At the same CO_2 level and the dry weights of roots and shoots increased concomitantly with NO_3^-–N proportion increase, and the roots became softer, browner, shorter and smaller with the increase of NH_4^+/NO_3^- ratio in the nutrient solutions. These results indicated that tomato seedling roots may benefit more from CO_2 enrichment when a higher NO_3^-–N proportion nutrient solution was supplied and that CO_2 enrichment did not mitigate the negative effects of high NH_4^+–N concentration (100%) on the tomato seedling. The CO_2 enrichment had little effect on the root/shoot ratio except for that in the 75% NH_4^+–N nutrient solution. Whereas the results revealed a trend that the root/shoot ratio increased with the enhancement of NH_4^+–N proportion. This suggests that NH_4^+/NO_3^- ratio has a larger effect on the growth of tomato seedlings with elevated CO_2 concentration than with the ambient concentration and dry matter seems to be preferentially allocated

Table 2 Effect of CO_2 concentration on the growth and development of tomato seedling roots with different NH_4^+/NO_3^- ratios

CO_2 concentration/$\mu L \cdot L^{-1}$	NH_4^+/NO_3^- ratio	dry weight of root/$g \cdot plant^{-1}$	dry weight of shoot/$g \cdot plant^{-1}$	root length/mm	root/shoot ratio
720	0:1	0.57 ± 0.04 a	5.44 ± 0.12 a	253 ± 1.30 bc	0.10 ± 0.00 e
	1:3	0.45 ± 0.01 b	3.79 ± 0.02 b	228 ± 0.63 d	0.12 ± 0.00 de
	1:1	0.42 ± 0.03 b	2.50 ± 0.14 e	233 ± 0.78 d	0.17 ± 0.00 b
	3:1	0.24 ± 0.04 d	1.76 ± 0.08 f	259 ± 0.35 ab	0.14 ± 0.02 cd
	1:0	0.06 ± 0.00 e	0.38 ± 0.01 h	170 ± 1.21 e	0.17 ± 0.01 b
360	0:1	0.32 ± 0.03 c	3.28 ± 0.29 c	239 ± 0.77 cd	0.10 ± 0.00 e
	1:3	0.41 ± 0.03 b	2.88 ± 0.01 d	254 ± 0.94 bc	0.14 ± 0.01 cd
	1:1	0.40 ± 0.01 b	2.51 ± 0.03 e	270 ± 0.72 a	0.16 ± 0.00 bc
	3:1	0.40 ± 0.05 b	1.45 ± 0.01 g	273 ± 0.35 a	0.28 ± 0.04 a
	1:0	0.06 ± 0.00 e	0.40 ± 0.02 h	170 ± 0.12 e	0.16 ± 0.01 bc
analysis of variance					
		dry weight of root	dry weight of shoot	root length	root/shoot ratio
NH_4^+/NO_3^- ratio		***	***	***	***
CO_2 concentration		***	***	***	***
NH_4^+/NO_3^- ratio × CO_2		***	***	***	***

Note: Means within a column followed by the different letter(s) are 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. *** means $P < 0.001$. This is the same for Table 3.

to roots when a higher NH_4^+–N proportion nutrient solution is supplied.

3.3 Effect of CO_2 concentration on some physiological indices of tomato seedling roots with different NH_4^+/NO_3^- ratios

The growth and vigor level of the root may directly impact the aboveground parts' growth, plant nutritional status and yield level. Root vigor is a comprehensive assessment index that reflects the metabolic activity level and the root absorbing ability. Total root absorbing area and active absorbing area are also important indices to reflect the aspects of the root absorbing ability.

CO_2 concentration and NH_4^+/NO_3^- ratio as well as their interactions have significant effects on root vigor, total root absorbing area and active absorbing area (Table 3). Under the elevated CO_2 concentration, root vigor increased by 14.1%, 6.8% and 18.9%, respectively, in 0%, 50% and 75% NH_4^+–N nutrient solution, whereas it decreased by 0.9% and 6.5%, respectively, in 25% and 100% NH_4^+–N nutrient solution, compared to the ambient concentration. Total root absorbing area increased by 12.9%, 7.2%, 10.3% and 4.2%, respectively, in 0%, 25%, 50% and 75% NH_4^+–N nutrient solution, and decreased by 11.0% in 100% NH_4^+–N nutrient solution. Root active-absorbing area increased by 1.1%, 9.6%, 18.9% and 11.3%, respectively, in 0%, 25%, 50% and 75% NH_4^+–N nutrient solution, and decreased by 15.6% in 100% NH_4^+–N nutrient solution. Under the elevated CO_2 concentration, root vigor, total root absorbing area and active absorbing area increased to the maximum when 100% NO_3^-–N nutrient solution was supplied, whereas it increased to the maximum with 75% NO_3^-–N nutrient solution under the ambient CO_2 concentration. In other treatments, the root vigor, total root absorbing area and active absorbing area increased concomitant with the NO_3^-–N proportion increase in the nutrient solutions. In the different NH_4^+/NO_3^- ratio (0:1, 1:3, 1:1, 3:1, 1:0) treatments, compared to the former treatment with latter treatment, the root vigor increased by 5.7%, 9.2%, 19.6% and 22%, respectively, the total root absorbing area increased by 8.4%, 8.2%, 25.6% and 131.7%, respectively, and the root active-absorbing area increased by 12.7%, 8.8%, 34.6% and 245.0%, respectively, with the elevated CO_2 concentration, whereas the root vigor increased by −8.1%, 17.6%, 33.2% and 18.8%, respectively, the total root absorbing area increased by 2.9%, 11.4%, 18.7% and 98.0%, respectively, and the root active-absorbing area increased by 11.2%, 18.0%, 26.0% and 161.7%, respectively, with the ambient CO_2 concentration. These results indicated that the growth, vigor, total root absorbing area and actively absorbing area were significantly affected both by CO_2 concentration and NH_4^+/NO_3^- ratio.

4 Discussion and conclusions

4.1 pH

The results of this study indicated that the elevated CO_2 concentration can promote the growth and nutritive absorption of tomato seedlings and enlarge the varying range of solution pH. At both CO_2 levels, the varying range of pH narrowed in the 100% NH_4^+–N nutrient solution and was larger than that of the increase in 100% NO_3^-–N nutrient solution. This, possibly due to the NO_3^-–N assimilation, occurred not only in the roots, but also in other parts. At the rhizosphere, only about 1/3 of released OH^- was excreted out of the plants. These may lead to the narrow pH variation under the NO_3^-–N nutrient solution than under the NH_4^+–N nutrient solution (Zhang, 1998).

Table 3 Effect of CO_2 concentration on some physiological indices of tomato seedling roots with different NH_4^+/NO_3^- ratios

CO_2 concentration /$\mu L \cdot L^{-1}$	NH_4^+/NO_3^- ratio	root vigor system/ (TTC $mg \cdot h^{-1} \cdot g^{-1}$, FW)	total absorbing area /$m^2 \cdot plant^{-1}$	active absorbing area /$m^2 \cdot plant^{-1}$
720	0:1	0.53 ± 0.004 a	1.63 ± 0.009 a	1.06 ± 0.006 a
	1:3	0.50 ± 0.007 b	1.50 ± 0.009 b	0.94 ± 0.006 b
	1:1	0.46 ± 0.005 c	1.39 ± 0.022 c	0.86 ± 0.010 c
	3:1	0.38 ± 0.008 e	1.11 ± 0.074 e	0.64 ± 0.016 e
	1:0	0.25 ± 0.008 h	0.48 ± 0.046 f	0.19 ± 0.008 h
360	0:1	0.46 ± 0.005 c	1.44 ± 0.022 bc	0.95 ± 0.024 b
	1:3	0.50 ± 0.007 b	1.40 ± 0.019 c	0.86 ± 0.007 c
	1:1	0.43 ± 0.003 d	1.26 ± 0.042 d	0.72 ± 0.013 d
	3:1	0.32 ± 0.004 f	1.06 ± 0.062 e	0.58 ± 0.020 f
	1:0	0.27 ± 0.004 g	0.54 ± 0.004 f	0.22 ± 0.002 g

analysis of variance

	root vigor system	total absorbing area	active absorbing area
NH_4^+/NO_3^- ratio	***	***	***
CO_2 concentration	***	***	***
NH_4^+/NO_3^- ratio × CO_2	***	***	***

4.2 Root physiological characteristics

The acidification of the nutrient solution caused by NH_4^+–N uptake was presumed to be the main reason for root growth and development inhibition (Olsthoorn et al., 1991). In this experiment, the acidification by NH_4^+–N uptake inhibited both of the growth of the roots and the aboveground parts.

Yang et al. (2006) found that the elevated CO_2 concentration significantly decreased the root vigor, total root absorbing area and active absorbing area. However, Wei et al. (2000) got the inverse results. Our data indicated that the elevated CO_2 concentration could increase the root vigor, total root absorbing area and active absorbing area, which was supported by the results in fruit vegetables (Wei et al., 2000). These discrepancy results mentioned above can be explained by the variety of the crops, growth conditions and environmental factors.

4.3 Dry matter distribution

Different organs of tomato seedlings exhibit different responses to the elevated CO_2 concentration. At both CO_2 levels, the root-to-shoot ratio increased concomitantly with the NH_4^+–N proportion increase in the nutrient solution. This result may be attributed to: (1) At higher NH_4^+–N proportion, dry matter may be preferentially allocated to the roots, indicating that tomato seedlings were adapted to the NH_4^+–N stress concentration from toxicity by adjusting internal resources allocation. Optimal partitioning of the dry weight among the plant organs is a most important way to cope with the environmental variation and optimize the resources capture to maximize plant growth rate (Brouwer, 1983; McConnaughay and Coleman, 1999; Reynolds and Thornley, 1982; Wilson, 1988); (2) This study indicates that the root-to-shoot ratio increased along with a concomitant increase in the NH_4^+–N proportion of the nutrient solutions. This may be due to the inhibitory effect of higher NH_4^+–N on the shoot growth which was larger than that on the roots. It can also be explained that NH_4^+–N could increase the dry matter content per unit leaf area, and thereby drastically reduced the dry matter distribution to the roots in soil culture (Cramer and Lewis, 1993; Troelstra et al., 1995). These results reveal that the responses of crops to the NH_4^+–N concentration were varied considerably with the type of plants and culture conditions.

Taken together, our data confirmed that the tomato seedlings grow best in 100% NO_3^-–N nutrient solution with elevated CO_2 concentration. However, CO_2 enrichment does not alleviate the harmful effects of high NH_4^+–N concentration in nutrient solutions on the tomato root system.

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