

Response of photosynthesis in the leaves of cucumber seedlings to light intensity and CO₂ concentration under nitrate stress

Xiaoyu YANG^{1,3}, Xiufeng WANG^{1,2,*}, Min WEI^{1,2}

¹College of Horticulture Science and Engineering, Shandong Agricultural University, Tai'an 271018, Shandong, PEOPLE'S REPUBLIC OF CHINA

²State Key Laboratory of Crop Biology, Tai'an 271018, Shandong - PEOPLE'S REPUBLIC OF CHINA

³Graduate School of Horticulture, Chiba University, Matsudo 271-8510, Chiba - JAPAN

Received: 08.12.2009

Accepted: 26.04.2010

Abstract: The effects of 2 nitrate levels, 14 (CK) and 140 mmol L⁻¹ (T), on the leaf gas exchange variables of cucumber (*Cucumis sativus* L. cv. Xintaimici) seedlings grown in hydroponic culture were investigated. Photosynthetic light- and CO₂-response curves from CK and T seedlings were determined and used for the analysis of photosynthetic capacity. The results showed that nitrate stress resulted in a significant reduction of net photosynthesis of T seedlings compared with CK. At the same time, the apparent quantum yield, light-saturated net photosynthesis, carboxylation efficiency, and CO₂-saturated net photosynthesis in nitrate-stressed cucumbers also decreased significantly with the increase of treatment time. At 12 days, the apparent quantum yield, light-saturated net photosynthesis, carboxylation efficiency, and CO₂-saturated net photosynthesis in nitrate-stressed cucumbers were 47%, 60%, 64%, and 54% lower than CK, respectively. The relative effect of stomatal resistance on photosynthesis (S%) in nitrate-stressed cucumber seedlings increased significantly during the first 8 days and returned to the level of CK thereafter. This evidence indicates that not only stomatal but also nonstomatal limitations might be involved in the reduction of net photosynthetic rate in nitrate-stressed seedlings.

Key words: CO₂-response curve, cucumber, light-response curve, nitrate stress

Introduction

Nitrogen, often a limiting resource for plant growth and development, is needed in larger amounts by plants than any other mineral element because it is a constituent of macromolecules such as proteins. The availability of nitrogen is thus a significant determinant of crop yield (Foyer & Noctor, 2002). Complicating this for agriculture is the fact that often

less than 50% of nitrogen fertiliser applied is ultimately utilised by crops, because nitrate ions are highly mobile and not absorbed by soil colloid (Allison, 1966). To satisfy the nitrogen demand, farmers often add nitrogen in large quantities to maintain an adequate level in the rhizosphere (Zhu et al., 2005). This excessive use of nitrogen fertiliser has resulted in undesirable conditions such as the

* E-mail: xfwang@sdau.edu.cn

accumulation of nitrate in plants and soil. The large accumulation of nitrogen in the soil has contaminated the ground water (Barker & Mills, 1980) and resulted in secondary soil salinisation in protected farmland because of a lack of leaching by rainfall and strong evaporation of soil water (Kitamura et al., 2006).

China has the largest area of protected crops and is now the leading country in the world for protected agriculture, including multispans greenhouses, solar lean-to greenhouses, and plastic tunnels (Jiang & Qu, 2000). However, secondary soil salinisation has seriously limited sustainable development of agricultural production in protected farmland of China (Yu et al., 2005). According to previous studies (Yu et al., 2005; Ju et al., 2007), accumulation of ions in protected farmland is greatly different from ordinary soil salinisation. In protected farmland, the main cations and anions are Ca²⁺, K⁺, and NO₃⁻, while Na⁺ and Cl⁻ are the main forms of ions in ordinary soil salinisation.

In the past several years, many studies about salt stress to plants have been done, but most of them have focused on NaCl (Zhu, 2002; Debouba et al., 2007; Munir and Aftab, 2009; Stepien & Johnson, 2009). There have been few investigations about nitrate stress in horticultural crops. Cucumber is one of the most important horticultural crops, and it has been reported that excessive accumulation of nitrate widely inhibits the growth and development of cucumber in protected farmland of China (Lü et al., 2007; Gao et al., 2008a, 2008b), while the underlying mechanisms are still not well understood. Photosynthesis is the fundamental metabolic process and plays a critical role in plant growth and development. This process is very sensitive to environmental stresses. Drought (Lauteri et al., 1997), salt stress (Bongi & Loreto, 1989), and leaf aging (Loreto et al., 1994) all result in inhibition of photosynthesis because of the reduction of conductance to CO₂ diffusion in the leaf mesophyll (Delfine et al., 1999). However, little information about changes of photosynthesis under nitrate stress exists. Therefore, we studied how excessive nitrate influenced photosynthesis in the leaves of cucumber seedlings. Responses of photosynthetic rate in nitrate-stressed cucumber seedlings to different levels of light intensity and CO₂ concentration were measured under greenhouse conditions.

Materials and methods

Plants, growth conditions, and experimental design

Cucumber (*Cucumis sativus* L. cv. Xintaimici, mid-tolerant to salinity stress) seeds were sterilised with sodium hypochlorite containing 5% active HOCl for 5 min and then soaked for 12 h in deionised water after being washed 5 times. The soaked seeds were raised in well-washed quartz sand in the greenhouse of Shandong Agricultural University and irrigated with tap water. When plants had one fully expanded leaf, they were removed from the trays and their roots were washed with tap water to remove the substrate, and then they were transplanted to hydroponic boxes (40 cm × 30 cm × 12 cm, 8 plants/box) with a complete cucumber nutrient solution (pH 6.0-6.5) containing Ca(NO₃)₂ 3.5 mmol mol⁻¹, KNO₃ 7 mmol mol⁻¹, KH₂PO₄ 1 mmol mol⁻¹, MgSO₄ 2 mmol mol⁻¹, H₃BO₃ 0.05 mmol mol⁻¹, Na₂FeEDTA 0.05 mmol mol⁻¹, MnSO₄ 0.01 mmol mol⁻¹, ZnSO₄ 0.0008 mmol mol⁻¹, CuSO₄ 0.0003 mmol mol⁻¹, and (NH₄)₂MoO₇ 0.02 mmol mol⁻¹ (Guo, 2004). The nutrient solutions in all of the hydroponic boxes were continually aerated with an electric pump and completely renewed every 4 days. The osmotic potential of the nutrient solution was measured with a vapour pressure osmometer (Model No. 5520, Wescor Inc., Logan, UT, USA) according to the method of Zou (1997). The experiment was carried out under greenhouse conditions with an air temperature of 25-30 °C during the day and 18-25 °C during the night.

When the seedlings had developed 3 fully expanded leaves, extra nitrate was dissolved in the nutrient solution directly. The excess nitrate test was carried out in a completely randomised design with a split plot arrangement of 3 replications, providing 8 plants per replication. Two treatments were applied (Table 1):

(CK) complete nutrient solution (control), and

(T) complete nutrient solution + Ca(NO₃)₂ 31.5 mmol L⁻¹ + KNO₃ 63 mmol L⁻¹.

At days 0, 4, 8, and 12 of exposure to treatment, the second fully expanded leaves, counted from the top of seedlings, were sampled for the measurement of photosynthetic light- and CO₂-response curves.

Table 1. Nitrate concentration and osmotic potential of nutrient solution.

Treatment	Ca(NO ₃) ₂ (mmol L ⁻¹)	KNO ₃ (mmol L ⁻¹)	NO ₃ ⁻ (mmol L ⁻¹)	Osmotic potential before treatment (MPa)	Osmotic potential after treatment for 3 days (MPa)
CK	3.5	7	14	-0.256	-0.218
T	35	70	140	-0.570	-0.567

Determination of photosynthetic light-response curve

Photosynthetic light-response curves were measured in the greenhouse using the Ciras-II Portable Photosynthesis System (Ciras-II, PP Systems, UK). The photosynthetic chamber provided a leaf area of 2.5 cm², a leaf temperature of 25 °C, relative humidity of 90%, leaf-to-air vapour pressure of 200 mbar, and a CO₂ concentration of 380 μmol mol⁻¹. Leaves were given 10 min in the chamber to reach equilibrium, which was assessed visually by graphing a strip chart of photosynthesis over time. Light curves were measured using the instrument's AutoProgram function. Measurements were taken at irradiance levels of 1400, 1200, 1000, 800, 600, 500, 400, 300, 200, 150, 100, and 50 μmol m⁻² s⁻¹. A minimum wait time of 90 s was used at each irradiance level.

Photosynthetic parameters derived from the light-response curves were determined according to the method described before (Richardson & Berlyn, 2002). Net photosynthesis under the highest irradiance level (1400 μmol m⁻² s⁻¹) was taken to be the light-saturated rate of net photosynthesis. The apparent quantum yield of photosynthesis was calculated as the slope of the light-response curve across the 4 lowest irradiance levels (50, 100, 150, and 200 μmol m⁻² s⁻¹).

Determination of photosynthetic CO₂-response curve

The response of net photosynthesis to intercellular CO₂ concentration was determined in the greenhouse using the Ciras-II Portable Photosynthesis System (Ciras-II, PP Systems, UK). The photosynthetic chamber provided a leaf area of 2.5 cm², a leaf temperature of 25 °C, relative humidity of 90%, leaf-to-air vapour pressure of 200 mbar, and irradiance of 1000 μmol m⁻² s⁻¹. Leaves were given 10 min in the

chamber to reach equilibrium. Measurements were taken at atmospheric CO₂ levels of 50, 100, 150, 200, 250, 300, 350, 400, 600, 800, 1000, 1200, 1400, 1600, and 1800 μmol mol⁻¹.

Net photosynthesis values were plotted against the respective intercellular CO₂ concentrations to produce a response curve. Photosynthetic parameters derived from the CO₂-response curve data were determined according to the method described before (Harrison et al., 2001; Habermann et al., 2003). Net photosynthesis under the highest intercellular CO₂ level was taken to be the CO₂-saturated rate of net photosynthesis. Net photosynthesis and corresponding intercellular CO₂ values for the linear portion of the response curve were subjected to linear regression analysis in order to determine the carboxylation efficiency of net photosynthesis.

The relative effect of stomatal resistance on photosynthesis (S%) was estimated by the following equation (Farquhar & Sharkey, 1982):

$$S\% = [(AC_i - AC_a)/AC_i] \times 100,$$

where *AC_a* represented the net photosynthesis at an atmospheric CO₂ concentration of 350 μmol mol⁻¹ and *AC_i* was the net photosynthesis when the intercellular CO₂ concentration was set at 350 μmol mol⁻¹ (Table 2).

Table 2. Corresponding atmospheric CO₂ concentration.

	Atmospheric CO ₂ concentration (μmol mol ⁻¹)	
	CK	T
Day 0	456	457
Day 4	450	490
Day 8	444	455
Day 12	475	459

Statistical Analysis

Data were analysed with Origin Program (Version 8.0, OriginLab Corporation, MA, USA) and presented as means of 3 replicates ± standard errors.

Results and discussion

Figure 1 and Figure 2 show changes of photosynthetic light- and CO₂-response curves in the leaves of cucumber seedlings under nitrate stress. Across the whole treatment course, nitrate stress resulted in a significant reduction of net photosynthesis of T seedlings compared with CK seedling. The lowered net photosynthesis of nitrate-stress seedlings is probably related to low water potential around the rhizosphere (Table 1), which may block the water absorbance of roots and induce the closure of stomata (Terzi et al., 2010). At a lower light intensity, increasing

irradiance resulted in a proportional increase in photosynthesis for both treatments (Figure 1), indicating that photosynthesis was limited by the amount of available light. The initial slope of the light-response curve based on absorbed light (quantum yield) describes the efficiency with which light is converted into fixed carbon. When the light-response curve is based on incident light, the leaf's absorbance also determines the quantum yield; this initial slope is called the apparent quantum yield of photosynthesis for the leaves (Lambers et al., 2008). In CK seedlings, this value was 0.0384 μmol CO₂ mol⁻¹ quanta at day 0, 0.0374 μmol CO₂ mol⁻¹ quanta at day 4, 0.0328 μmol CO₂ mol⁻¹ quanta at day 8, and 0.0339 μmol CO₂ mol⁻¹ quanta at day 12, whereas it was 0.0356, 0.0235, 0.0204, and 0.0179 μmol CO₂ μmol⁻¹ quanta in T seedlings (Figure 3). These values correspond to the respective quantum yields of 26.0, 26.7, 30.5, and 29.5

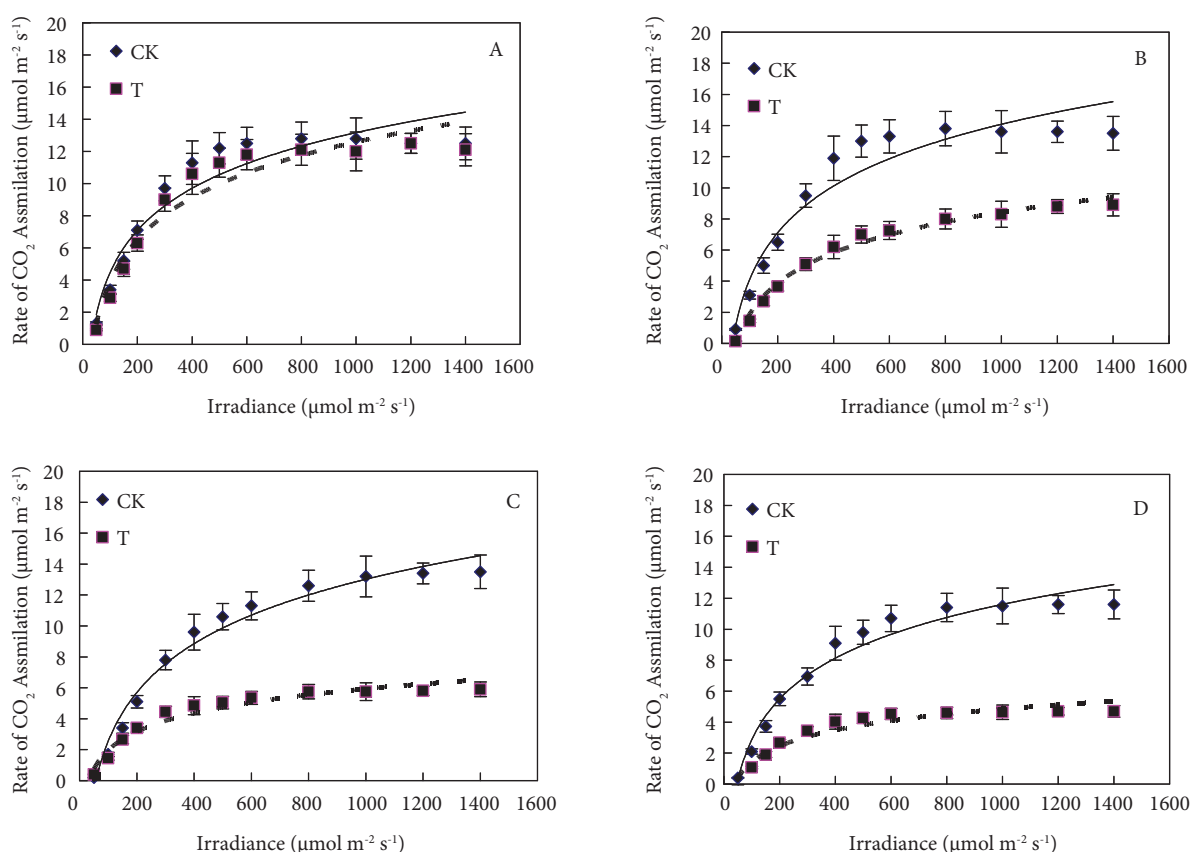


Figure 1. Photosynthetic light-response curve for leaves of cucumber seedlings grown in nutrient solution containing 14 (CK) and 140 mmol L⁻¹ (T) nitrate at days 0 (A), 4 (B), 8 (C), and 12 (D) after treatment, respectively. Vertical bars represent the standard errors (n = 3).

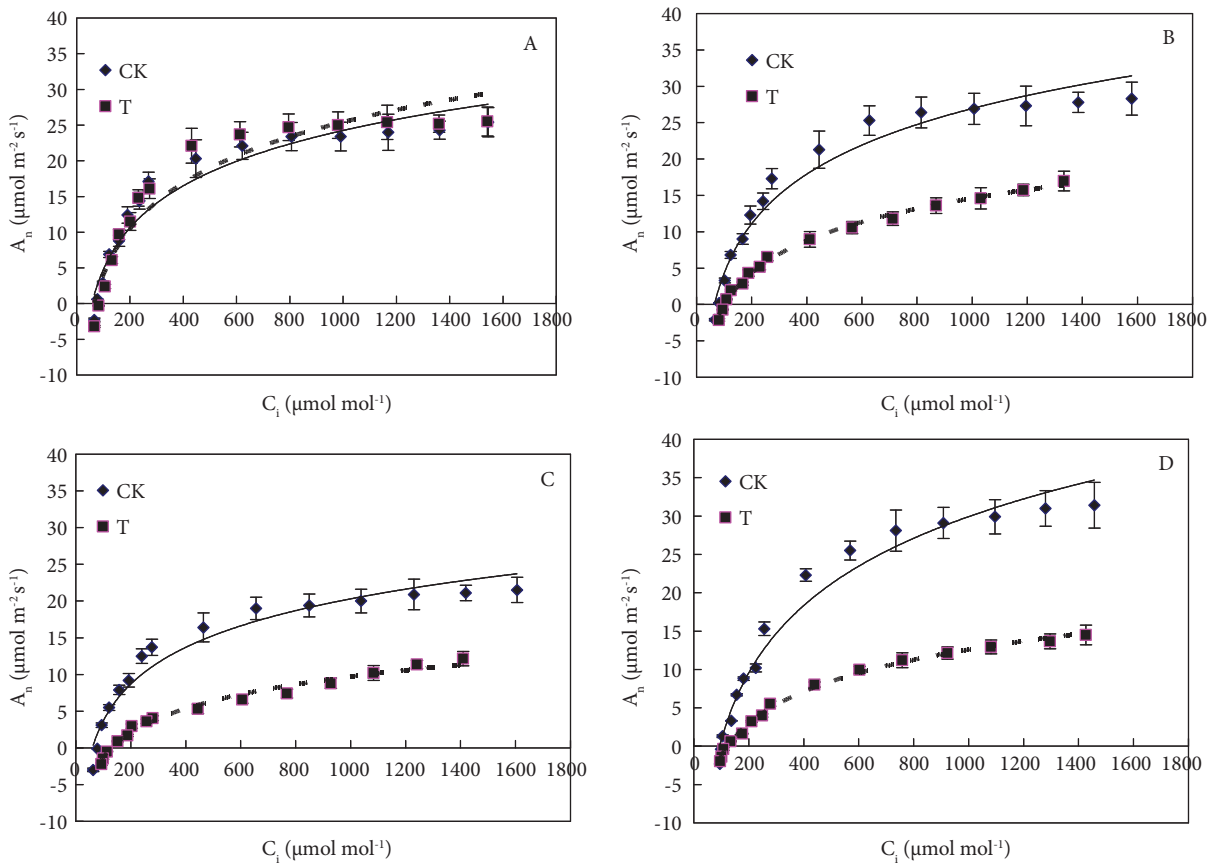


Figure 2. Net photosynthesis (A_n) versus intercellular CO_2 concentration (C_i) for the leaves of cucumber seedlings grown in nutrient solution containing 14 (CK) and 140 mmol L^{-1} (T) nitrate at days 0 (A), 4 (B), 8 (C), and 12 (D) after treatment, respectively. Vertical bars represent the standard errors ($n = 3$).

$\mu\text{mol quanta } \mu\text{mol}^{-1} \text{CO}_2$ in the leaves of CK seedlings, and 20.1, 42.6, 49.0, and 56.0 $\mu\text{mol quanta } \mu\text{mol}^{-1} \text{CO}_2$ in the leaves of T seedlings. These results suggest that the Calvin cycle efficiency, in terms of utilisation of ATP and NADPH, is lowered in nitrate-stressed leaves with the increase of treatment time. At higher light intensity, the photosynthetic response to irradiance started to level off and reached a saturation plateau (Figure 1). The light saturation point in CK seedlings was 600–800 $\mu\text{mol m}^{-2} \text{s}^{-1}$, whereas it significantly decreased to 400–500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for T seedlings at the end of the treatment course (Figure 1), indicating that factors such as electron transport reaction, Rubisco activity, and metabolism of triose phosphates had become more limiting in plants treated with 140 mmol L^{-1} of nitrate. Moreover, the light-saturated CO_2 assimilation rate of seedlings treated with 140 mmol L^{-1} of nitrate significantly decreased with the increase of

treatment time (Figure 1). At day 12, the light-saturated CO_2 assimilation rate was 60% lower in T seedlings than CK seedlings.

The values of intercellular CO_2 concentration (C_i) in the leaves of nitrate-stressed cucumbers (T) were lower than CK at day 4, but higher than CK at days 8 and 12 (Figure 2). However, the calculation of C_i may not be reliable when CO_2 and water vapour fluxes are low, as occurred in T seedlings due to low water potential in the root medium (Table 1). For the calculation of C_i , the formula ($C_i = C_a - Pn (r_a' + r_s')$) was used. In this formula, C_a is the atmospheric CO_2 concentration, Pn is the rate of net photosynthesis, and r_a' and r_s' represent the diffusion resistance of the boundary layer and stomata for CO_2 . The r_a' is usually determined from the rate of evaporation of moist filter paper (Gaastra, 1959). The r_s' is estimated from the transpiration rate. The cuticular transpiration is

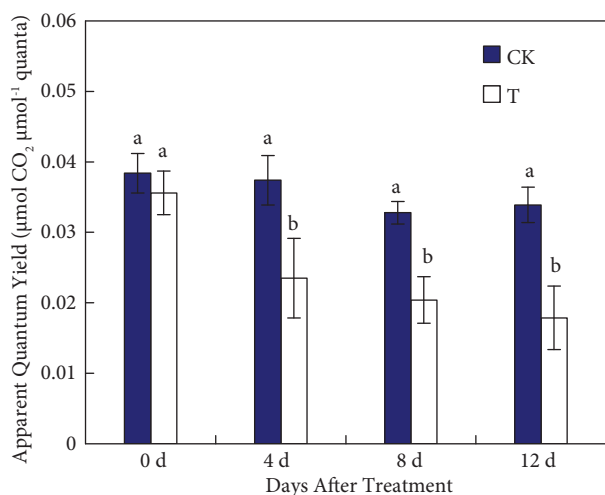


Figure 3. Apparent quantum yield for the leaves of cucumber seedlings grown in nutrient solution containing 14 (CK) and 140 mmol L⁻¹ (T) nitrate at days 0, 4, 8, and 12 after treatment, respectively. Vertical bars represent the standard errors (n = 3). Different letters indicate significant differences between the treatments at the 0.05 level by Duncan's new multiple range test.

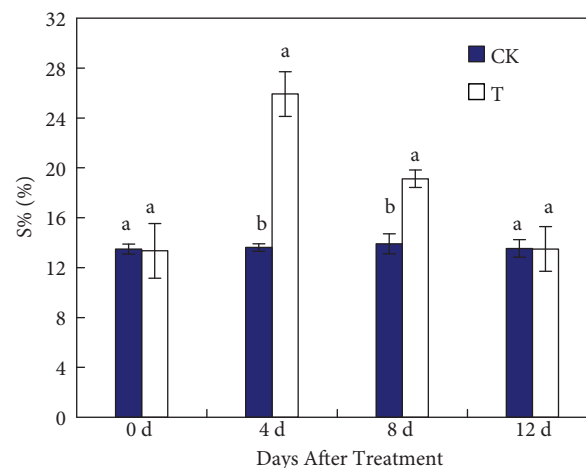


Figure 4. The relative effect of stomatal resistance on photosynthesis (S%) for the leaves of cucumber seedlings grown in nutrient solution containing 14 (CK) and 140 mmol L⁻¹ (T) nitrate at days 0, 4, 8, and 12 after treatment, respectively. Vertical bars represent the standard errors (n = 3). Different letters indicate significant differences between the treatments at the 0.05 level by Duncan's new multiple range test.

usually neglected, and the value of diffusion leaf resistance (r') is then substituted for r_a' in this formula (Hák & Nátr, 1984). In case the cuticular transpiration represents a significant constituent of total transpiration (e.g. under drought stress), neglecting it may cause C_i to be overestimated and thus mask some stomatal effects on the photosynthetic reduction (Cornic, 2000). In order to determine the effects of stomatal resistance on photosynthesis, S% has been investigated in the nitrate-stressed (T) cucumber seedlings, as well. The values of S% in the leaves of T seedlings significantly increased during the first 8 days, and then returned to the level of CK (Figure 4), indicating that the substrate for photosynthetic activity was not restricted under long-term nitrate stress. Therefore, the factor that may be involved in the reduction of the net photosynthetic rate in nitrate-stressed seedlings are not only stomatal limitations but also some photochemical and biochemical factors.

The CO₂-response curves from CK and T seedlings were submitted to logarithmic regression (Figure 2). The linear portions of the CO₂-response curves from both treatments were compared (Figure 2), and the carboxylation efficiency of nitrate-stressed seedlings

significantly decreased with the increase of treatment time (Figure 5). Electron transport took place through electron and proton transport chains in the photosynthetic membrane (Zeng et al., 2008). The decrease of water content in the leaves of nitrate-stressed cucumber seedlings could affect the rate of electron transport, since water was the provider of the electron transport chains (Gao, 2008b). A low rate of electron transport would significantly limit photosynthetic phosphorylation and the synthesis of NADPH, and then the regeneration of RuBP was limited (Harley, 1992). As a result, the carboxylation efficiency of T seedlings decreased by 64% with respect to CK at day 12. The significant decrease of carboxylation efficiency indicates that higher photorespiration may act in the seedlings treated with 140 mol L⁻¹ of nitrate. The photorespiration may be a protective mechanism by which plants can avoid photoinhibition, mainly in C3 plants (Hall & Rao, 1994), produce intercellular CO₂ (maintaining Rubisco activity), and consume strong oxidants like H₂O₂ by action of catalases (Lüttge et al., 1996). In addition, CO₂-saturated net photosynthesis of seedlings treated with 140 mmol L⁻¹ of nitrate significantly decreased

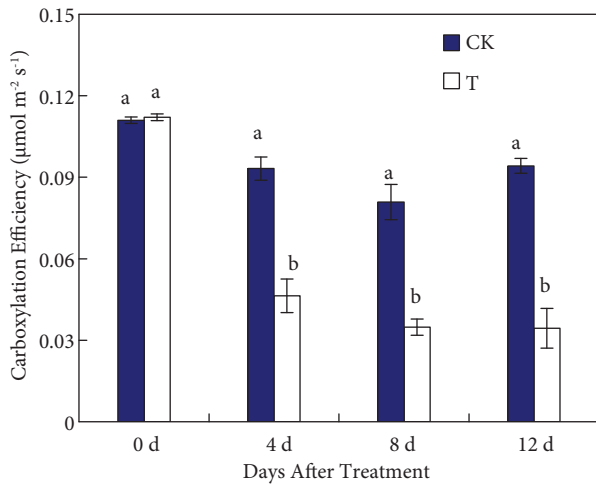


Figure 5. Carboxylation efficiency for the leaves of cucumber seedlings grown in nutrient solution containing 14 (CK) and 140 mmol L⁻¹ (T) nitrate at days 0, 4, 8, and 12 after treatment, respectively. Vertical bars represent the standard errors (n = 3). Different letters indicate significant differences between the treatments at the 0.05 level by Duncan's new multiple range test.

with the increase of treatment time (Figure 2). At day 12, CO₂-saturated net photosynthesis was 54% lower in T seedlings than CK seedlings.

All of these results of lower leaf gas exchange rates, coupled with the affected photosynthetic metabolism in nitrate-stressed cucumber seedlings, lead us to think that one of nitrate stress' mechanisms of action is occurring. Large amounts of nitrate accumulated in the soil result in low water potential, which blocks the water absorbance of roots and results in a lack of water supply to the mesophyll, thus influencing the stomatal opening and the photosynthetic biochemical reactions.

Acknowledgements

We thank Xintai Cucumber Research Institute of Xintai, China, for kindly providing plant materials. This work has been supported by the National Natural Science Foundation of China (grant no: 30471187).

References

- Allison FE (1966). The fate of nitrogen applied to soils. *Advan Agron* 18: 219-258.
- Barker AV & Mills HA (1980). Ammonium and nitrate nutrition of horticultural crops. *Hort Rev* 2: 395-423.
- Bongi G & Loreto F (1989). Gas-exchange properties of salt-stressed olive (*Olea europea* L.) leaves. *Plant Physiol* 90: 1408-1416.
- Cornic G (2000). Drought stress inhibits photosynthesis by decreasing stomatal aperture - not by affecting ATP synthesis. *Trends Plant Sci* 5: 187-188.
- Debouba M, Maàroufi-Dghimi H, Suzuki A, Ghorbel MH & Gouia H (2007). Changes in growth and activity of enzymes involved in nitrate reduction and ammonium assimilation in tomato seedlings in response to NaCl stress. *Ann Bot* 99: 1143-1151.
- Delfine S, Alvino A, Villani MC & Loreto F (1999). Restrictions to carbon dioxide conductance and photosynthesis in spinach leaves recovering from salt stress. *Plant Physiol* 119: 1101-1106.
- Farquhar GD & Sharkey TD (1982). Stomatal conductance and photosynthesis. *Annu Rev Plant Physiol* 33: 317-345.
- Foyer CH & Noctor C (2002). *Photosynthetic Nitrogen Assimilation and Associated Carbon and Respiratory Metabolism*. Berlin: Springer-Verlag.
- Gaastra P (1959). Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature and stomatal diffusion resistance. *Meded Landbouwhogeschool Wageningen* 59: 1-68.
- Gao QH, Wang XF, Shi QH, Yang FJ & Wei M (2008a). Effects of lanthanum on the plant growth and leaf anti-oxidative enzyme activities of cucumber seedlings under nitrate stress. *Chin J Appl Ecol* 19: 976-980.
- Gao QH, Wei M, Yang FJ, Shi QH, Wang XF & Zhang YH (2008b). The response of dry matter accumulation, turgor pressure and photosynthetic rate in cucumber seedlings to nitrate and ammonium nitrogen. *Plant Nutr Fert Sci* 14: 120-125.
- Guo SR (2004). *Soilless Culture*. Beijing: China Agricultural Press.
- Habermann G, Machado EC, Rodrigues JD & Medina CL (2003). CO₂ assimilation, photosynthetic light response curves, and water relations of 'Pêra' sweet orange plants infected with *Xylella fastidiosa*. *Braz J Plant Physiol* 15: 79-87.
- Hák R & Nátr L. (1984). The significance of cuticular transpiration for the calculation of intercellular CO₂ concentration. *Biologia Plantarum* 26: 74-76.
- Hall DO & Rao KK (1994). *Photosynthesis: Studies in Biology*. Cambridge: Cambridge University Press.
- Harley PC, Thomas RB, Reynolds JF & Strain BR (1992). Modelling photosynthesis of cotton grown in elevated CO₂. *Plant Cell Environ* 15: 271-282.
- Harrison EP, Olcer H, Lloyd JC, Long SP & Raines CA (2001). Small decreases in SSPase cause a linear decline in RuBP regeneration rate, but do not affect Rubisco carboxylation capacity. *J Exp Bot* 52: 1779-1784.

- Jiang WJ & Qu DY (2000). Present situation and suggestion for sustainable development of protected horticulture in mainland China. *Chin Agri Sci Bul* 16: 61-63.
- Ju XT, Kou CL, Christie P, Dou ZX & Zhang FS (2007). Changes in the soil environment from excessive application of fertilizers and manures to two contrasting intensive cropping systems on the North China Plain. *Environ Pollut* 145: 497-506.
- Kitamura Y, Yano T, Honna T, Yamamoto S & Inosako K (2006). Causes of farmland salinization and remedial measures in the Aral Sea basin—research on water management to prevent secondary salinization in rice-based cropping system in arid land. *Agric Water Manage* 85: 1-14.
- Lambers H, Chapin FS & Pons TL (2008). *Plant Physiological Ecology*. New York: Springer.
- Lauteri M, Scartazza A, Guido MC & Brugnoli E (1997). Genetic variation in photosynthetic capacity, carbon isotope discrimination and mesophyll conductance in provenances of *Castanea sativa* adapted to different environments. *Funct Ecol* 11: 675-683.
- Loreto F, Di Marco G, Tricoli D & Sharkey TD (1994). Measurements of mesophyll conductance, photosynthetic electron transport and alternative electron sinks of field grown wheat leaves. *Photosynth Res* 41: 397-403.
- Lü J, Wang XF, Wei M, Yang FJ, Gao QH, Du DL & Yang XY (2007). Effect of different salt treatments on growth and physiological characteristics of cucumber seedlings. *Plant Nutr Fert Sci* 13: 1123-1128.
- Lüttge U, Kluge M & Bauer G (1996). Les cytosomes In: *Botanique: Traité Fondamental*, pp. 137-145. Paris: Lavoisier, Tec & Doc.
- Munir N & Aftab F (2009). The role of polyethylene glycol (PEG) pretreatment in improving sugarcane's salt (NaCl) tolerance. *Turk J Bot* 33: 407-415.
- Richardson AD & Berlyn GP (2002). Spectral reflectance and photosynthetic properties of *Betula papyrifera* (Betulaceae) leaves along an elevational gradient on Mt. Mansfield, Vermont, USA. *Am J Bot* 89: 88-94.
- Stepien P & Johnson GN (2009). Contrasting responses of photosynthesis to salt stress in the glycophyte *Arabidopsis* and the halophyte *Thellungiella*: role of the plastid terminal oxidase as an alternative electron sink. *Plant Physiol* 149: 1154-1165.
- Terzi R, Sağlam A, Kutlu N, Nar H & Kadioğlu A (2010). Impact of soil drought stress on photochemical efficiency of photosystem II and antioxidant enzyme activities of *Phaseolus vulgaris* cultivars. *Turk J Bot* 34: 1-10.
- Yu HY, Li TX & Zhou JM (2005). Secondary salinization of greenhouse soil and its effects on soil properties. *Soils* 37: 581-586.
- Zeng W, Jiang YL, Li F & Zhou GS (2008). Responses of photosynthetic parameters of *Quercus mongolica* to soil moisture stresses. *Acta Ecologica Sinica* 28: 2504-2510.
- Zhu JH, Li XL, Christie P & Li JL (2005). Environmental implications of low nitrogen use efficiency in excessively fertilized hot pepper (*Capsicum frutescens* L.) cropping systems. *Agric Ecosys Environ* 111: 70-80.
- Zhu JK (2002). Salt and drought stress signal transduction in plants. *Ann Rev Plant Biol* 53: 247-273.
- Zou Q (1997). *Experiment Directions of Plant Physiology and Biochemistry*. Beijing: China Agricultural Press.