Available online at www.sciencedirect.com
ScienceDirect
Journal of Environmental Sciences 19(2007) 1361–1366
JOURNAL OF ENVIRONMENTAL SCIENCES
ISSN 1001-0742
CN 11-2629/X
www.jesc.ac.cn

Effects of lanthanum(III) on nitrogen metabolism of soybean seedlings under elevated UV-B radiation

CAO Rui[1], HUANG Xiao-hua[2], ZHOU Qing[1,*], CHENG Xiao-ying[1]

1. The Key Laboratory of Industrial Biotechnology, Ministry of Education, Southern Yangtze University, Wuxi 214036, China. E-mail: caorui128@163.com
2. College of Chemistry and Environment Science, Nanjing Normal University, Nanjing 210097, China

Received 1 February 2007; revised 26 March 2007; accepted 9 May 2007

Abstract

The hydroponic culture experiments of soybean bean seedlings were conducted to investigate the effect of lanthanum (La) on nitrogen metabolism under two different levels of elevated UV-B radiation (UV-B, 280–320 nm). The whole process of nitrogen metabolism involves uptake and transport of nitrate, nitrate assimilation, ammonium assimilation, amino acid biosynthesis, and protein synthesis. Compared with the control, UV-B radiation with the intensity of low level 0.15 W/m^2 and high level 0.45 W/m^2 significantly affected the whole nitrogen metabolism in soybean seedlings ($p < 0.05$). It restricted uptake and transport of NO_3^-, inhibited activity of some key nitrogen-metabolism-related enzymes, such as: nitrate reductase (NR) to the nitrate reduction, glutamine systhetase (GS) and glutamine synthase (GOGAT) to the ammonia assimilation, while it increased the content of free amino acids and decreased that of soluble protein as well. The damage effect of high level of UV-B radiation on nitrogen metabolism was greater than that of low level. And UV-B radiation promoted the activity of the anti-adversity enzyme glutamate dehydrogenase (GDH), which reduced the toxicity of excess ammonia in plant. After pretreatment with the optimum concentration of La (20 mg/L), La could increase the activity of NR, GS, GOGAT, and GDH, and ammonia assimilation, but decrease nitrate and ammonia accumulation. In conclusion, La could relieve the damage effect of UV-B radiation on plant by regulating nitrogen metabolism process, and its alleviating effect under low level was better than that under the high one.

Key words: lanthanum(III); UV-B radiation; soybean seedlings; nitrogen metabolism; alleviating effect

Introduction

Depletion of the stratospheric ozone layer causes increase of ultraviolet-B (UV-B, 280–320 nm) radiation reaching the earth's surface. This increase is likely to last in the foreseeable future with potential damage to agriculture, horticulture and forestry (Bilger *et al*., 2001; Kakani *et al*., 2003). The rare earth (RE) has been extensively used as micro-fertilizers in China for many years. Positive effects on crop yields of RE have been reported (Ni, 2002), in which RE could induce plant resistance to stress, such as ozone (An and Wang, 1994), drought (Ning, 1994), salt (Gao *et al*., 1995), acid rain (Ji *et al*., 2002), and heavy metals (Huang and Zhou, 2006). These facts inferred that RE could relieve the damage of plants contaminated by environment.

In the previous study, we found that RE could relieve the damage effect of UV-B radiation on the growth of rape seedlings, and the regulating effect is related to the improvement of photosynthesis (Liang *et al*., 2005) and antioxidant defense system (Liang *et al*., 2006a). We also found that RE could enhance the resistance of soybean seedling to UV-B radiation and relieve the damage effect of UV-B radiation on plants by regulating the synthesis of protecting compounds such as flavonoid (Liang *et al*., 2006b). However, more information is not available for the mechanisms of RE alleviating the damage effect of UV-B radiation in plant.

Nitrogen is an essential mineral element plants required mostly, and nitrate is the most important source of nitrogen for plants (Crawford and Glass, 1998). In nitrogen metabolism, nitrate is taken up and transported in plant, then NO_3^- is reduced to NO_2^-, and finally NO_2^- is converted to NH_4^+. NH_4^+-N is assimilated into amino acids, nucleic acids, proteins, chlorophylls, and other metabolites (Stitt *et al*., 2002). Obviously, nitrogen influences all levels of plant function, from metabolism to resource allocation, growth, and development. Since RE could alleviate the damage effect of UV-B radiation in plants, it might be relative with nitrogen metabolism.

In this study, we investigated the key enzymes of the nitrogen metabolism, nitrate reductase (NR), glutamine synthetase (GS), glutamate synthetase (GOGAT) and glutamate dehydrogenase (GDH) as well as their related

Project supported by the National Natural Science Foundation of China (No. 30570323) and the Foundation of State Developing and Reforming Committee (No. IFZ20051210). *Corresponding author. E-mail: zhouqeco@yahoo.com.cn.

substances (amino acid, soluble protein), which might provide more valuable information to clarify the mechanism of RE to alleviate damage effect of UV-B radiation in plants, and point out a new research direction for ecological protection of crops against UV-B radiation.

1 Materials and methods

1.1 Culturing of plant

The soybean (*Clycine* max.) seeds of "Kennong 18" were sterilized for 5 min by $HgCl_2$ (0.1%), and washed three times with deionized water. After being soaked for 4 h, seeds were placed in the dish underlaid with three pieces of filter paper and germinated in the incubator at 25±1°C. When the length of seedlings was about 2 cm, seedlings were transplanted into plastic pots (diameter 10 cm, 5/pot) filled with deionized water under the illumination of 8 klx (12 h/d), and aired twice every day. When the first leaf was developed, the seedlings were cultured in Arnon + Hogland's solution. The nutrient solution was renewed every 3 d for pH stabilization (pH 6.5). The seedlings with age of 5 weeks were treated by lanthanum (La) and UV-B radiation.

1.2 Treatment

The optimum concentration of $LaCl_3$ solution was 20 mg/L, which was determined in our preliminary experiment. The $LaCl_3$ solution was sprayed evenly on the leaves until drops began to fall. The same amount of distilled water was applied to another set as the control (CK). After 48 h, half of seedlings pretreated with La were placed under ultraviolet lamps.

Enhanced UV-B radiation was performed with 40 W UV-B lamps (Nanjing Lamp Factory), hanging perpendicularly over the plants. Two levels of UV-B radiation with low level 0.15 W/m^2 and high level 0.45 W/m^2 were investigated, which were calibrated by ultraviolet radiation (Photo-electricity Instrument Factory of Beijing Normal University). Seedlings were irradiated from 10:00 to 15:00 every day for 5 d. The height of lamps over the plants was adjusted to maintain consistent radiation intensity.

There were 6 sample sets in the experiments: control (sprayed with deionized water), La (sprayed with $LaCl_3$ solution), T_1 (irradiated with 0.15 W/m^2 UV-B), T_2 (irradiated with 0.45 W/m^2 UV-B), La+T_1 (sprayed with $LaCl_3$ solution and then exposed to 0.15 W/m^2 UV-B radiation) and La+T_2 (sprayed with $LaCl_3$ solution and then exposed to 0.45 W/m^2 UV-B radiation). There were 3 replicates for each set and 3 pots in every set.

1.3 Determination

The activity of nitrate reductase and content of NO_3^- were determined according to Zhang (1994). Activity of NADH-glutamate synthase was determined according to Singh and Srivastava (1986). Activity of NADH-glutamate dehydrogenase was conducted according to Kanamori *et al*. (1972). Activity of glutamine synthetase was according to Rhode *et al*. (1975). Soluble protein content was determined according to Bradford (1976). The content of free amino acid was determined by amino acid autoanalyzer (HP1100, Agilent Co., U.S.).

1.4 Statistical analysis

Data reported are the mean±SD of three independent experiments. Means in independent experiments were tested for significance using lower-significant-difference (LSD, $P < 0.05$).

2 Results and discussion

2.1 Effects of La on nitrate absorption and assimilation in soybean seedlings under UV-B radiation

NR is a rate-limiting enzyme in nitrate assimilation and catalyses NO_3^- reduction to NO_2^- (Campbell, 1999), which eventually affects the growth and organic nitrogen status of plants. As a typical nitrate-induced enzyme, NR activity is limited by the concentration of NO_3^- in leaves.

Figure 1 shows the dynamic effects of La on NO_3^- content and NR activity in soybean seedlings with 6 treatments for 10 d. The trend of Fig.1a was similar to that of Fig.1b. Compared with the controls, NO_3^- content and NR activity was decreased from the 1st day to the day 5 under UV-B radiation, and increased continuously after the UV-B radiation was removed. The results indicated that the absorption and assimilation of the important mineral for plants nitrate were significantly inhibited under UV-B radiation, especially under the high level. Correspondingly, the growth of seedlings was restrained. However, when the plants were pretreated with La solution, the decrease range of nitrate content was smaller than that under UV-

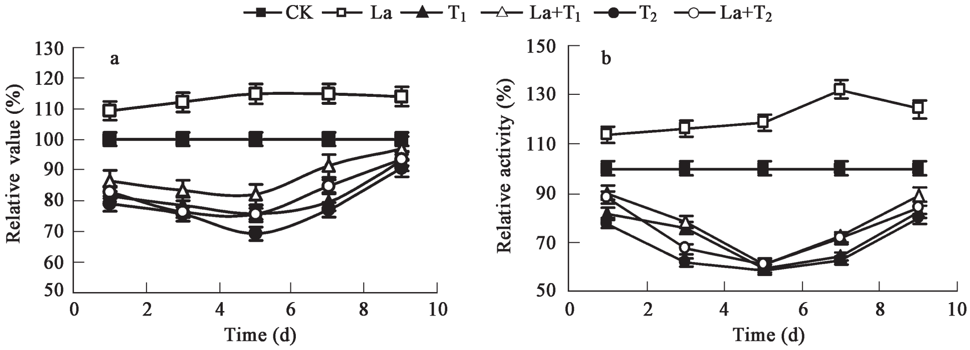

Fig. 1 Effects of La on NO_3^- content (a) and NR activity (b) in soybean seedlings under UV-B radiation. T_1: irradiated with 0.15 W/m^2 UV-B; T_2: irradiated with 0.45 W/m^2 UV-B.

B radiation, especially under low level. It indicated that La could promote the uptake and transport of nitrate in plants, which might be related to the fact that La has a positive effect on the transpiration of seedlings, promoting the uptake and movement of water and mineral nutrients (Liang *et al*., 2005). Thus, the assimilation of nitrate could be improved by inducing NR activity and increasing nitrate in plants.

NR is a nitrate-induced enzyme and the increase of nitrate content will promote the NR activity. It might be relative with why NR activity increased by La pretreatment in the experiments. Further, NR activity needs to reduce power (NADH, NADPH), which mainly comes from glycose metabolism. And there is a close metabolic coordination between nitrate assimilation and CO_2-photosynthetic assimilation (Foyer *et al*., 1998). La could enhance every important step of photosynthesis process in plants (Liang *et al*., 2006c), increase the content of soluble sugar and starch, and indirectly improve photosynthesis on NR activity under UV-B radiation.

2.2 Effects of La on ammonia assimilation in soybean seedlings under UV-B radiation

2.2.1 Activities of GOGAT, GS, and GDH, the content of Glu, Gln, and total amino acids

The cycle of GS and GOGAT is considered to be the main pathway of ammonia assimilation in plants. The enzymatic reactions are as follows (Lee and Chen, 1988).

$$\text{L-glutamate + ammonia + ATP} \longrightarrow \text{L-glutamine + ADP + Pi} + H_2O\text{(GS)} \quad (1)$$

$$\text{L-glutamine} + \alpha\text{-oxoglutarate + NADH} \longrightarrow \text{2L-glutamate} + NAD^+\text{(GOGAT)} \quad (2)$$

where, ATP is adenosine triphosphate; ADP is adenosine diphosphate; Pi is H_3PO_4; NADH is reduced nicotinamide adenine dinucleotide; NAD^+ is nicotinamide adenine dinucleotide; and GDH is an anti-adversity reductase, which catalyses the reaction between α-oxoglutarate and glutamate.

$$\alpha\text{-oxoglutarate} + NH_3 + NAD(P)H \longleftrightarrow \text{L-glutamate} + H_2O + NAD(P)^+ \quad (3)$$

Although the function of GDH has not been studied thoroughly, GDH can operate in adverse situations such as carbon stress, weak light or dark, ammonia toxicity (Goss *et al*., 2001).

In Table 1, the sequence of change range in NADH-GOGAT activity was La (+15.8%) > Control (CK) > La+T_1 (–7.8%) > T_1 (–12.6%) > La+T_2 (–31.0%) > T_2 (–34.7%). Compared with the controls, the activity of NADH-GOGAT was restrained by UV-B radiation badly. The changes of GS activity were similar to those of GOGAT, which might be related to the feedback adjustment of reaction production (glutamine) in the GS/GOGAT cycle.

The change range of NADH-GDH activity was different to that of GS and GOGAT. In Table 1, the sequence of GDH activity was La+T_1 (+47.0%) > T_1 (+30.4%) > La (+18.3%) > CK > La+T_2 (–9.0%) > T_2 (–12.8%). Both low level of UV-B radiation and La promoted GDH activity while high level of UV-B radiation dramatically decreased GDH activity. Under low level of UV-B radiation, it was very important to enhance the GDH activity when the activity of GS and GOGAT decreased sharply leading to the accumulation of ammonia in plants. High concentration ammonia was toxic to plants, and the increase of GDH activity could reduce this toxicity. Reversely, under high level of UV-B radiation, GDH structure or some related genes might be damaged, decreasing GDH activity finally. Compared with UV-B treatment, the activities of GS, GOGAT and GDH increased with La pretreatment. Thus, La had positive effects on reducing ammonia toxicity and alleviating damage of UV-B radiation to plants.

Free amino acids, especially glutamic acid (Glu) and glutamine (Gln), are the products of ammonia assimilation and may participate in protein synthesis. In Table 1, the sequence of total free amino acids content was La (3.3846) < CK (3.7771) < La+T_1 (4.0867) < T_1 (4.4968) < La+T_2 (6.3317) < T_2 (7.2260). When the free amino acids were exposed to UV-B radiation, their contents increased. Many proteins were decomposed under UV-B radiation and T_2 treatment was the worst in our experiment (Tang *et al*., 2004). The change of Glu content was La+T_2 (0.7708) < La (0.7907) < CK (0.9275) < T_2 (0.9720) < La+T_1 (0.9929) < T_1 (1.2044). Compared with UV-B treatment, La pretreatment could reduce Glu content significantly. Theoretically, Glu content increases with intensified UV-B radiation due to decomposition of protein and inhibition of enzymes activity. However, our experiment was T_2 < T_1, which might be caused by the strengthened pathway of Glu consumption such as transamination and decomposition. Compared with UV-B treatment, the content of total free amino acids and Glu decreased largely with La pretreatment, proving that La could promote activity of GS and GOGAT. As temporary storage of the ammonia, Gln is very important to adverse environment. The sequence

Table 1 Effects of La on the activities of GOGAT, GS and GDH, and the content of Glu, Gln and total amino acid in soybean seedlings under UV-B radiation

Treatment	GOGAT	GS	GDH	Glu (mg/g)	Gln (mg/g)	Total amino acid (mg/g)
CK	16.20±1.56b (100.0)	56.80±1.11a (100.0)	13.17±0.82c (100.0)	0.9275	0.1053	3.7771
La	18.77±0.76a (115.8)	60.26±0.45a (106.1)	15.59±0.57b (118.3)	0.7907	0.1095	3.3846
T_1	14.16±0.63c (87.4)	50.36±1.17b (88.7)	17.17±0.91a (130.4)	1.2044	0.1354	4.4968
La+T_1	14.94±0.33bc (92.2)	52.31±0.48b (92.1)	19.37±1.10a (147.0)	0.9929	0.1244	4.0867
T_2	10.59±0.72d (65.3)	42.12±0.56c (74.1)	11.49±0.55d (87.2)	0.9720	0.2313	7.2260
La+T_2	11.18±0.43d (69.0)	43.72±2.04c (76.9)	11.98±0.56d (91.0)	0.7708	0.1956	6.3317

Results are means ± SD (n=3); the values in the bracket are related values and the letters are related to difference; values in each column followed by the same letter did not differ significantly (P < 0.05) by LSD.

of Gln content was CK (0.1053) < La (0.1095) < La+T_1 (0.1244) < T_1 (0.1354) < La+T_2 (0.1956) < T_2 (0.2313). UV-B radiation increased the content of Gln, which was helpful to alleviate ammonia toxicity.

2.2.2 Dynamic effects of La on the activities of GOGAT and GS

Figure 2a shows that GOGAT activity with La pretreatments was much higher than the other treatments while the promoting effect of La pretreatment was significant. Under UV-B radiation, the enzyme activity decreased gradually, reaching the bottom on the day 5 (decrease range: T_1 12.6% and T_2 34.7%). But the enzyme activity increased immediately after the radiation was removed. Up to the day 11, the enzyme activity with T_1 treatment was close to CK while that with T_2 treatment increased to 86.3% of CK. Compared with UV-B treatment, GOGAT activity increased to different extents after pretreated with La. Further, the average increase range with La+T_1 treatment was a slightly higher than La+T_2.

UV-B radiation could significantly affect GOGAT in soybean leaves, decreasing its activity rapidly. The alleviative effect of La on seedlings under low level of UV-B radiation was better than the high one, which might be due to the fact that La could stabilize GOGAT structure and decrease inactivation of chemical modification, the amount of hydrolysis, excessive oxygenic radical and NH_3 under UV-B radiation.

The dynamic changes of GS activity showed the same trend as GOGAT (Fig.2b). Fig.2 indicates that UV-B radiation restrained the activities of both GOGAT and GS, the key enzymes of nitrogen metabolism. The formation of Glu and Gln was inhibited as well as the synthesis of protein, finally affecting growth of seedlings. La pretreatment could alleviate dramatic decrease of GOGAT and GS activity, and plants with La showed better recovery after UV-B radiation was removed. That is, the resistance to UV-B radiation was strengthened in plants with La. The contents of Glu, Gln and total free amino acids in leaves increased significantly under UV-B radiation while the GS and GOGAT activities decreased. Thus, we deduced that the increase of free amino acids content was not related to ammonia assimilation but protein decomposition mainly. It was coincident with the result that UV-B radiation caused the decrease of protein content in our experiment.

2.2.3 Dynamic effects of La on the activity of GDH

GDH has lower affinity to NH_3. Although GDH pathway is not the main pathway of ammonia assimilation, it is very important to the situation of ammonia with high concentration. It plays an important role in the fast ammonia assimilation and relieves the toxicity due to ammonia with high concentration in plants.

Figure 3a shows that in T_1 treatment without radiation, GDH activity increased obviously and kept high level after 5 d, and in T_2 treatment with radiation, GDH activity increased quickly in 6 h. Further, the enzyme activity decreased rapidly with continual radiation, then increased after the UV-B radiation was removed. The enzyme activity with La pretreatment was much higher than the other treatments. The low level of UV-B radiation promoted GDH activity evidently while the high level inhibited GDH activity. Under elevated UV-B radiation, catabolism was strengthened and ammonia content was increased in plants. GDH activity increased to relieve ammonia toxicity. Fig.3a shows that the enzyme activity of T_1 treatment was greater than CK while that of T_2 was lower than T_1. It might be caused by that GDH was inactivated with chemical modification or the hydrolysis was strengthened under high level of UV-B radiation. Compared with the corresponding treatments, GDH activity was increased with La pretreatment, and the promoting effect with La on enzyme activity was more significant under low level of UV-B radiation. We concluded that La could enhance the GDH activity and capability of ammonia assimilation in plants, alleviating damage of plant under UV-B radiation.

2.2.4 Effects of La on the soluble protein content

Many studies show that the UV-B radiation cause the decrease of soluble protein content of plants, especially the Ribulose bi-phosphate carboxylase-oxyenase (Rubisco), a key enzyme of photosynthesis (Jordan *et al*., 1992). Rubisco occupies over 50% content of total soluble protein in leaves, thus the extensive decrease of soluble protein content might be related to the damage of Rubisco under UV-B radiation. Fig.3b shows that the change trend of soluble protein content was similar to NR (Fig.1b), and the soluble protein content with La treatment was more than CK. According to our previous study (Huang *et al*., 2005), La could promote carbon metabolism to satisfy requirement of energy (ATP), power reduction (NADH,

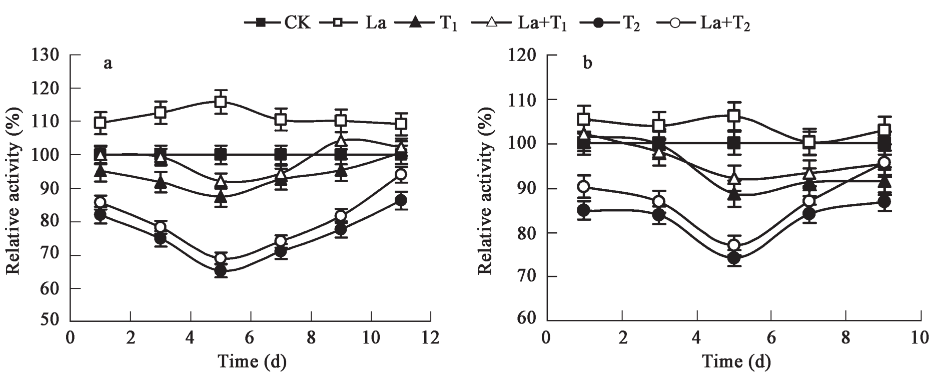

Fig. 2 Effects of La on the activities of GOGAT (a) and GS (b) in soybean seedlings under UV-B radiation. T_1, T_2 are the same as that in Fig.1.

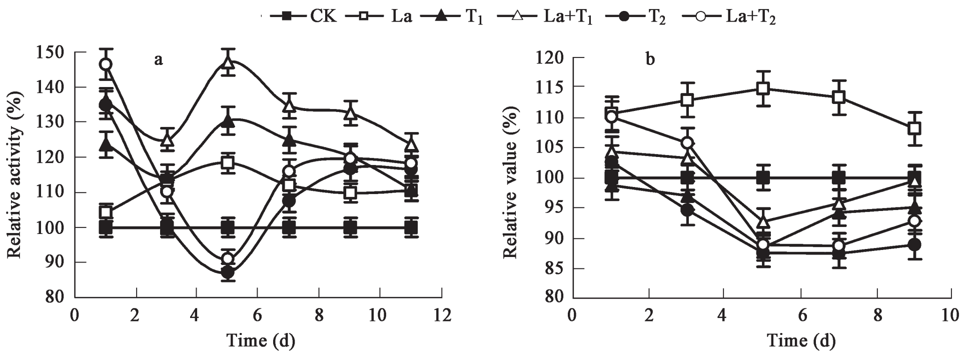

Fig. 3 Effects of La on GDH activity (a) and soluble protein content (b) in soybean seedlings under UV-B radiation. T_1, T_2 are the same as that in Fig.1.

NADPH), and carbon skeleton (α-oxoglutarate) in nitrogen assimilation. Compared with the controls, the soluble protein content with La+UV-B and UV-B treatments were increased on the 1st day, then decreased sharply to the bottom, and finally kept on increasing gradually after UV-B radiation was removed. The soluble protein decreased more slowly with La+UV-B treatment than UV-B treatment in radiation period (1–5 d) while it with La+UV-B treatment increased more quickly in the recovery period (6–9 d). According to the changes of soluble protein during the initial 5 d, La might promote protein synthesis and weaken damage effect under UV-B radiation. The changes of soluble protein in the recovery period indicated that La could accelerate protein synthesis. And the alleviative effect with La+T_1 treatment was better than with La+T_2 treatment. Aforementioned facts showed that La could promote the protein synthesis in plants and relieve the damage of UV-B radiation as well.

3 Conclusions

The resistance to UV-B radiation could be strengthened with La pretreatment. In seedling leaves under UV-B radiation, La could promote the uptake and assimilation of nitrate, which alleviated the restraint of nitrogen metabolism.

The activity of key enzymes related to nitrogen metabolism decreased under UV-B radiation. The NO_3^- reduction and ammonia assimilation were badly restrained under UV-B radiation. After plants was pretreated with La, enzymes activity was increased. In short, ammonia assimilation was improved with La pretreatment.

GDH could increase ammonia assimilation rapidly under UV-B radiation, which could compensate decrease of ammonia assimilation. And GDH activity increased with La pretreatment, which promoted the capability of ammonia assimilation and alleviated the toxicity of ammonia accumulation.

Under UV-B radiation, the content of free amino acids increased obviously mainly due to the decomposition of soluble protein. And La could promote protein synthesis in plants, and relieve damage of UV-B radiation.

In conclusion, La could alleviate the damage of UV-B radiation during the growth of soybean seedlings by regulating nitrogen metabolism. And the alleviative effect of La on plants under low level of UV-B radiation was better than the high one.

References

An L Z, Wang X L, 1994. Effect of ozone on growth of spring wheat and the prevention of rare earth to ozone injury[J]. Acta Ecologica Sinica, 14(1): 95–98.

Bilger W, Johnsen T, Schreiber U, 2001. UV-excited chlorophyll fluorescence as a tool for the assessment of UV-protection by the epidermis of plants[J]. Journal of Experimental Botany, 52(363): 2007–2014.

Bradford M M, 1976. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding[J]. Analytical Biochemistry, 72(7): 248–254.

Campbell W H, 1999. Nitrate reductase structure, function and regulation: bridging the gap between biochemistry and physiology[J]. Annu Rev Plant Physiol Plant Mol Biol, 50: 277–303.

Crawford N M, Glass D M A, 1998. Molecular and physiological aspect of nitrate uptake in plants[J]. Trends Plant Sci, 3: 389–395.

Foyer C H, Valadier M, Migge A, Becker T W, 1998. Drought-induced effects on nitrate reductase activity and mRNA and on coordination of nitrogen and carbon in maize leaves[J]. Plant Physiol, 117(1): 283–292.

Gao Y, Zhang R M, Guo X H, 1995. Effects of RE soaking seeds under salt coercing on the peroxidation of membrance of *Coixlacryma-jobi* seedings[J]. Chinese Rare Earths, 16: 35–36.

Goss T J, Perez-Matos A, Bender R A, 2001. Roles of glutamate synthase, *glt*BD and *glt*F in nitrogen metabolism of *Escherichia coli* and *Klesiella aerogenes*[J]. Journal of Bacteriology, 183(22): 6607–6619.

Huang X H, Zhou Q, 2006. Alleviation effect of lanthanum on cadmium stress in seedling hydroponic culture of kidney bean and corn[J]. Journal of Rare Earths, 24(2): 248–252.

Huang X H, Zhou Q, Zhang G S, 2005. Advances on rare earth application in pollution ecology[J]. Journal of Rare Earths, 23(1): 5–11.

Ji H N, Huang X H, Zhou Q *et al*., 2002. UV-Vis spectroscopy study on interaction between microperoxidase-11 and Pr Ion under acid rain radiation[J]. Journal of Rare Earths, 20(2): 541–546.

Jordan B R, Chow W S, Anderson J M, 1992. Changes in mRNA levels and polypeptide subunits of ribulose-1,5-biophosphate carboxylase in response to supplementary ultraviolet-B radiation[J]. Plant, Cell Environment, 15: 91–98.

Kakani V G, Reddy K R, Zhao D *et al*., 2003. Field crop responses to ultraviolet-B radiation[J]. Agricultural and Forest Meteorology, 120(1): 191–218.

Kanamori T, Konishi S, Takhashi E, 1972. Inducible formation of glutamate dehydrogenase in rice plants roots of the addition of ammonia to the media[J]. Physiologia Plantarum, 26: 1–6.

Lee C, Chen L B, 1988. Dynamic behavior of endoplasmic reticulum in living cells[J]. Cell, 54(1): 37–46.

Liang C J, Huang X H, Zhou Q, 2005. Effects of rare earths on plant under elevated ultraviolet-B radiation radiation: I. Effect of cerium on growth and photosynthesis in rape seedlings exposed to supplementary ultraviolet-B radiation[J]. Journal of Rare Earth, 23(5): 569–575.

Liang C J, Huang X H, Tao W Y *et al*., 2006a. Effect of rare earths on plants under supplementary ultraviolet-B radiation: II. Effect of cerium on antioxidant defense system in rape seedlings under supplementary ultraviolet-B radiation[J]. Journal of Rare Earths, 24(3): 364–368.

Liang B, Huang X H, Zhang G S *et al*., 2006b. Effect of lanthanum on plants under supplementary Ultraviolet-B radiation: effect of lanthanum on flavonoid contents in soybean seedlings exposed to supplementary Ultraviolet-B radiation[J]. Journal of Rare Earths, 24(5): 613–616.

Liang C J, Huang X H, Zhou Q, 2006c. Effect of cerium on photosynthetic characteristics of soybean seedling exposed to supplementary ultraviolet-B radiation[J]. Journal of Environmental Sciences, 18(6): 1147–1151.

Ning J B, 1994. Reserarch on the effects of rare earth elements on improve crops yield[J]. Chinese Rare Earth, 15(1): 63–65.

Ni J Z, 2002. Bioinorganic chemistry of rare earth elements[M]. Beijing: Science Press. 14, 56, 68.

Rhodes D, Rendo G A, Stewart G R, 1975. The control of glutamine synthetase level in *Lemna minor* L.[J]. Planta, 125(3): 201–211.

Singh R D, Srivastava H S, 1986. Increase in glutamate synthase (NADH) activity in maize seedlings in response to nitrate and ammonium nitrogen[J]. Physiology Plant, 66(3): 413–416.

Stitt M, Müller C, Matt P *et al*., 2002. Steps towards an integrated view of nitrogen metabolism[J]. J Exp Bot, 53(370): 959–970.

Tang L N, Lin W X, Liang Y Y *et al*., 2004. Effects of enhanced ultraviolet-B radiation on soluble protein and nucleic acid in rice leaves[J]. Chinese Journal of Eco-Agriculture, 12(1): 39–42.

Zhang Z L, 1994. Guide to experiments of plants physiology[M]. Beijing: High Educational Press. 41–43.