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ARTICLE

Effects of Exogenous Epibrassinolide on Photosynthetic Characteristics in Tomato (*Lycopersicon esculentum* Mill) Seedlings under Weak Light Stress

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The effects of three concentrations (0.1, 0.01, 0.001 mg/kg) of exogenous 24-epibrassinolide on leaf photosynthesis, chlorophyll content, chlorophyll fluorescence, and parameters of light response curve in tomato seedlings under 150 μmol·m^{-2}·s^{-1} weak light stress were studied, with two tomato cultivars, 'Zhongza9', tolerant, and 'Zhongshu6', sensitive to weak light stress. The results showed that the net photosynthetic rate (Pn), maximal photochemical quantum efficiency of PSII (Fv/Fm), light saturation point (LSP), and dark respiration rate (Rd) decreased remarkably under weak light, but the chlorophyll content, especially chlorophyll *b* (chlb) content, increased obviously compared with normal light intensity control. However, exogenous 24-epibrassinolide alleviated the decrease of leaf Pn and Fv/Fm and induced the further increase of chlb content as well as the further decrease of Rd and chla/chlb under weak light stress, which indicated that exogenous 24-epibrassinolide could enhance plant tolerance to weak light and diminish damage from weak light. However, the optimum concentrations were different between the two cultivars; 0.1 mg/kg 24-epibrassinolide showed the best induction effects in 'Zhongshu6', and the best level for 'Zhongza9' was 0.01 mg/kg 24-epibrassinolide.

KEYWORDS: 24-Epibrassinolide; tomato; weak light stress; photosynthesis; chlorophyll fluorescence

INTRODUCTION

Single-roof solar greenhouses were the predominant facilities for growing tomatoes (*Lycopersicon esculentum* Mill) during the winter and spring in China, and compared with even-span and multispan greenhouses in developed countries, their light transmittance was lower; in addition, the tomato is a light-loving plant, and it demands high light intensity for normal growth due to its originating from tropic and subtropic regions in southern America. Thus, poor light has become a main limit in tomato protected production, especially for overwintering cultivation in northern China. The basic way to relieve the poor light inhibition is breeding tomato cultivars tolerant to weak light, yet there are not any real tolerant cultivars on the market currently. At present, laying light-reflecting film, artificial lighting, and pruning are mainly used to improve the light conditions in protected facilities; however, the cost of the former two measures is high and the latter method works slowly, so it was hard to overcome the poor light condition in protected cultivation.

Chemical regulation technique is a commonlu used effective technology in horticultural cultivation. According to Gaba and Black (1983) (*1*), exogenous hormones could simulate light to regulate plant growth and development, which indicated that hormones might function as the second messenger in light signal transmission. Therefore, it will be an effective way to enhance the plant adaptability to weak light and improve plant quality and quantity by plant growth regulators.

Brassinolides (BRs, $C_{48}H_{48}O_6$) are a group of new plant hormones with high activity, which were first isolated from the pollen of the rape plant (*Brassica napus* L.) by Grove in 1979 (*2*). As the sixth group of phytohormones, they influence varied developmental processes such as germination of seeds, rhizogenesis, growth, flowering, fruiting, and senescence (*3*).

Neff et al. separated the *CYP72B1* gene, which could strengthen plant reaction to BRs, in 1999; reverse genetics research showed that the gene regulated plants' reaction to changes in the environment by regulating BR level, and thus BR might be a plastic promoting hormone, which makes plant adapt to the change of environment. This indicated that BR had more potential application in improving plant antistress ability (*4*). Recent studies have suggested BRs could enhance plant resistance to multiple stresses, such as water stress, temperature stress, salt stress, hypoxia stress, pathogen stress, and heavy metal stress (*5*−*10*), but research about its effects on weak light stress is rare.

More than 90% of plant biomass comes from photosynthesis, and the decrease of dry matter production caused by low net photosynthetic rate under weak light is the basic reason why weak light stress inhibits plant growth and development. In this experiment effects of different concentrations of 24-epibrassinolide on photosynthetic characteristics were measured to investigate whether exogenous 24-epibrassinolide could improve plants'

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tolerance to weak light stress in the light-loving tomato, so as to provide a theoretical foundation for establishing a new method to overcome weak light in protected cultivation and suggest the optimal 24-epibrassinolide concentration for applying and, at the same time lay a theoretical basis for, further studying the molecular mechanism of BR improving plants' resistance to weak light stress.

MATERIALS AND METHODS

Materials Cultivation. Two genotypes of tomato were used in this experiment: 'Zhongza9' (IVF, CAAS, Beijing, China), tolerant to weak light, and 'Zhongshu6' (IVF, CAAS, Beijing, China), sensitive to weak light. Tomato seeds were sown in plugs with a mixture of peat moss and vermiculite (v/v = 1:1) as culture substrate on September 3, 2007. At the phase of three fully expanded leaves in tomato seedlings, three concentrations of 24-epibrassinolide (Sigma) were applied to the foliage of selected uniform seedlings, 12 plants for each treatment.

Weak Light Treatment. As soon as the fluid was absorbed, and there were no water drops on the leaf surface, the seedlings were divided into two groups. One group was moved to a NY-2000 Phytotron (2 m × 2 m × 2 m, Zhongnong Yituo, Beijing, China) to be raised under 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ weak light provided by white fluorescent lamps for 10 h photoperiods at 25 °C and 14 h dark periods at 18 °C; the relative humidity was 75%, including the plants sprayed with distilled water (stress), 0.1 mg/kg 24-epibrassinolide (stess + 0.1 mg/kg), 0.01 mg/kg 24-epibrassinolide (stress + 0.01 mg/kg), and 0.001 mg/kg 24-epibrassinolide (stress + 0.001 mg/kg). The other group (control) including the plants sprayed with distilled water was moved to another NY-2000 Phytotron to be raised under 450 $\mu mol \cdot m^{-2} \cdot s^{-1}$ white fluorescent light with the same other conditions described above.

Photosynthesis and Chlorophyll Fluorescence Measurement. Plant photosynthesis and chlorophyll fluorescence were tested with the second fully expanded leaf under the growing point, on the first, third, fifth, and seventh days of weak light stress, using an LI-6400 portable photosynthesis system and a 6400-40 fluorescence leaf chamber (LICOR); four plants were used for each treatment. Fo and Fm were tested after 2 h of dark adaptation of tomato seedlings, and Fv/Fm was given by the equation Fv/Fm = (Fm − Fo)/Fm.

Chlorophyll Content Measurement. The second fully expanded leaf under the growing point was sampled on the fifth day of stress to measure chlorophyll content with an 80% acetone extraction method (*11*) using a UV-2102PC/PCS ultraviolet spectrophotometer (UNICO, Shanghai, China),; three plants were used for each treatment.

Light Response Curve Measurement. Light response curve was tested on the eighth day of stress with the second fully expanded leaf under the growing point. Pn was measured at 1500, 1200, 900, 600, 400, 250, 150, 50, and 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetic active radiation (PAR) under 400 $\mu mol \cdot mol^{-1}$ CO_2 concentration, 60% relative humidity, and 25 °C in leaf chamber. Data fitting was performed with the equation $y = ax^2 + bx + c$ (x represents PAR, y represents Pn) with EXCEL, and from this we could get Amax and LSP. Pn under 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PAR was used to simulate the equation $y = ax + b$ (x represents PAR, y represents Pn) with EXCEL, and from this we got Rd.

Statistical Analyses. The experiment was repeated three times in a randomized block design. The results presented in the tables and figures are the mean of three replications, and means were compared using the least significant difference (LSD, $P < 0.05$), except that the data of the light response curve were the mean of two replicates.

RESULTS

Effects of Exogenous 24-Epibrassinolide on Leaf Pn under Weak Light Stress. The most direct role of light on plants is photosynthesis; it supplies necessary energy for the formation of assimilatory ability, activates key enzymes involved in photosynthesis, and is an essential condition for the formation of chlorophyll and the development of chloroplast. At the same time photomorphogenesis was controlled by light signals through light receptors, so the most direct change is photosynthesis after the change of light intensities.

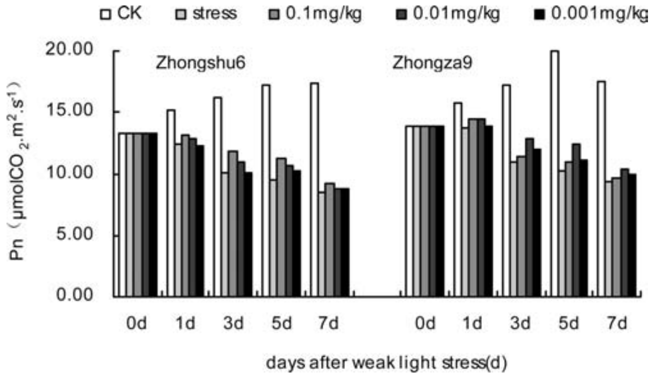

Figure 1. Effects of exogenous 24-epibrassinolide on leaf Pn in tomato seedlings under weak light stress.

Figure**1** shows that weak light stress significantly decreased leaf Pn of two cultivars; furthermore, leaf Pn decreased gradually with the increase of stress time, but Pn of 'Zhongza9', tolerant to weak light, was higher than that of the sensitive cultivar 'Zhongshu6'. At the same time, exogenous 24-epibrassinolide effectively alleviated the decrease of Pn under weak light.

On the first day of stress, there was no remarkable difference in Pn between each treatment under weak light in either 'Zhongshu6' or 'Zhongza9', but on the third, fifth, and seventh day of stress, all concentrations of 24-epibrassinolide alleviated the decline of Pn in the two cultivars to different degrees. Among the three concentrations, 0.1 mg/kg 24-epibrassinolide showed the best effect in 'Zhongshu6', the Pn of which was remarkably higher than that of nontreated stressed plants by 16.7, 18.8, and 8.5% on the third, fifth, and seventh days of stress respectively, higher than those of 0.01 and 0.001 mg/kg 24-epibrassinolide treatments, and reached significant levels on the third day. In contrast, 0.01 mg/kg 24-epibrassinolide increased leaf Pn in 'Zhongza9' mostly, and its Pn was obviously higher than that of nontreated stressed plants by 17.5, 21.7, and 11.1% on the third, fifth, and seventh days of stress and obviously higher than those of the other two concentrations; however, there was no obvious difference in Pn between the other two concentrations.

This indicated that exogenous 24-epibrassinolide could maintain a better photosynthetic metabolic level of tomato seedlings under weak light, but the optimal concentrations were different between cultivars of different genotypes.

Effects of Exogenous 24-Epibrassinolide on Fv/Fm under Weak Light Stress. Fv/Fm represents the maximum photochemical efficiency of PSII, and it is an important index and probe to reflect the degree of environmental stress. **Figure 2** indicates that Fv/Fm of each treatment under weak light of two cultivars reduced obviously compared with normal light control, but 'Zhongza9' showed higher Fv/Fm than 'Zhongshu6'. Simultaneously, exogenous 24-epibrassinolide induced the increase of Fv/Fm in both cultivars under weak light.

On the first and third days of stress, there was no obvious difference in Fv/Fm among various treatments under weak light in 'Zhongshu6', and on the fifth and seventh days of stress, Fv/Fm of all three concentrations was obviously higher than that of nontreated stressed plants; moreover, the 0.1 mg/kg treatment showed obviously higher Fv/Fm than 0.01 and 0.001 mg/kg treatments on the fifth day, which indicated that the 0.1 mg/kg 24-epibrassinolide treatment got the best effects on alleviating the decrease of Fv/Fm in 'Zhongshu6'.

However, the 0.01 mg/kg treatment showed the best induction effect in 'Zhongza9', the Fv/Fm of which was significantly higher than that of nontreated stressed plants by 0.8, 0.9, and 0.8% on

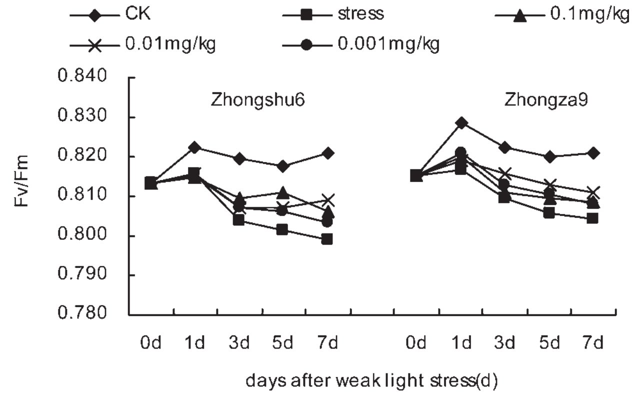

Figure 2. Effects of exogenous 24-epibrassinolide on Fv/Fm in tomato seedlings under weak light stress.

Table 1. Effects of 24-Epibrassinolide on Chlorophyll Content in Leaf on the Fifth Day of Weak Light Stress[a]

cultivar	treatment	chl(a+b) ($mg \cdot g^{-1}$ of FW)	chla ($mg \cdot g^{-1}$ of FW)	chlb ($mg \cdot g^{-1}$ of FW)	chla/chlb
Zhongshu6	CK	1.95 c	1.40 b	0.55 b	2.64 a
	stress	2.47 b	1.47 a	1.00 a	1.48 b
	0.1 mg/kg	2.56 a	1.46 a	1.11 a	1.32 c
	0.01 mg/kg	2.54 ab	1.46 a	1.08 a	1.37 c
	0.001 mg/kg	2.51 ab	1.47 a	1.05 a	1.40 bc
Zhongza9	CK	1.82 d	1.34 b	0.48 c	2.98 a
	stress	2.44 c	1.46 a	0.97 b	1.55 b
	0.1 mg/kg	2.49 c	1.46 a	1.03 b	1.43 b
	0.01 mg/kg	2.68 a	1.45 a	1.22 a	1.19 c
	0.001 mg/kg	2.61 b	1.46 a	1.15 a	1.27 c

[a] Different letters within the same column indicate significant difference ($P < 0.05$).

the third, fifth, and seventh days, and significantly higher than those of the 0.1 and 0.001 mg/kg treatments on the third and seventh days; simultaneously, no significant difference in Fv/Fm was observed between 0.1 and 0.001 mg/kg treatments, but their Fv/Fm values were higher than that of nontreated stressed plants.

Effects of Exogenous 24-Epibrassinolide on Chlorophyll Content under Weak Light Stress. Chlorophyll has an important role in light harvesting and transportation in photosynthesis, and its content directly influences the strength of photosynthesis. Table**1** suggests that the content of chla, chlb, and chl(a+b), especially chlb content, of all treatments under weak light increased remarkably compared with normal light control, and the chla/chlb ratio greatly decreased; these were adaptive responses of tomato seedlings to weak light stress, and the range in 'Zhongza9' was bigger. At the same time, all concentrations of 24-epibrassinolide induced the further increase of chlb and the further decrease of chla/chlb under weak light, which indicated that exogenous 24-epibrassinolide could induce the enhancement of this adaptive response under weak light.

Similar to the former results, the 0.1 mg/kg treatment showed better induction effects in 'Zhongshu6', the chl(a+b) content of which was obviously higher than that of nontreated stressed plants by 4.0%, and its chla/chlb ratio was obviously lower than that of nontreated stressed plants by 10.5%; simultaneously, the 0.1 mg/kg treatment showed higher chl(a+b) content and lower chla/chlb than the other two concentrations, but there was no significant difference among these three concentrations. However, 0.01 and 0.001 mg/kg treatments showed better induction effects in 'Zhongza9', the chlb and chl(a+b) contents of which were obviously higher than those of nontreated stressed plants (9.8 and 7.1%, respectively) and the 0.1 mg/kg treated plants, whereas chla/chlb was obviously lower than that of nontreated stressed plants (23.3 and 18.0%, respectively) and the 0.1 mg/kg treated plants.

Table 2. Effects of 24-Epibrassinolide on Leaf LSP, Amax, and Rd in Tomato Seedlings under Weak Light Stress

cultivar	treatment	LSP ($\mu mol \cdot m^2 \cdot s^{-1}$)	Amax (μmol of $CO_2 \cdot m^2 \cdot s^{-1}$)	Rd (μmol of $CO_2 \cdot m^2 \cdot s^{-1}$)
Zhongshu6	CK	1570	25.4	1.32
	stress	1120	13.9	0.65
	0.1 mg/kg	1200	15.5	0.39
	0.01 mg/kg	1100	12.2	0.42
	0.001 mg/kg	1105	13.4	0.41
Zhongza9	CK	1555	24.6	1.15
	stress	1115	13.9	0.46
	0.1 mg/kg	1061	11.5	0.39
	0.01 mg/kg	1160	14.9	0.17
	0.001 mg/kg	1130	13.7	0.20

Effects of Exogenous 24-Epibrassinolide on LSP, Amax, and Rd under Weak Light Stress. LSP, Amax, and Rd of all treatments under weak light obviously decreased compared with normal light control; meanwhile, Rd of 'Zhongza9' was lower than that of 'Zhongshu6', as shown in **Table 2**. The decrease of Rd could reduce plant consumption of photosynthetic assimilates, which was an adaptation reaction of tomato seedlings to weak light stress.

Rd values of 0.1, 0.01, and 0.001 mg/kg treatments decreased by 39, 35, and 37%, respectively, compared with nontreated stressed plants of 'Zhongshu6'. At the same time, LSP and Amax of only the 0.1 mg/kg treatment were higher than those of nontreated stressed plants. Compared with 'Zhongshu6', three concentrations decreased leaf Rd in 'Zhongza9' more under weak light stress by 16, 64, and 57%, respectively. The decreased range of 0.01 and 0.001 mg/kg treatments was much bigger. Moreover, LSP and Amax of only the 0.01 mg/kg treatment were higher than those of nontreated stressed plants in 'Zhongza9'. This indicated that 0.1 mg/kg 24-epibrassinolide had better induction effects in 'Zhongshu6' on this adaptive response to weak light, and the optimal concentration in 'Zhongza9' was 0.01 mg/kg.

DISCUSSION

Effects of Exogenous 24-Epibrassinolide on Leaf Phtosynthesis under Weak Light Stress. Pn is an important exterior mark of photosynthetic metabolism level in plants; its improvement is a comprehensive outcome of the increase of light using efficiency, the acceleration of CO_2 transportation, and the enhancement of CO_2 fixation, and the improvement of Pn under stresses could enhance plant antistress ability. However, chlorophyll fluorescence dynamics is an ideal inner probe to measure injury to the photosystem from various stresses (*12*,*13*); it can reflect the relationship between the environment and plant photosynthetic physiological state rapidly and sensitively. In recent years, chlorophyll fluorescence analysis has been developed into a kind of new, fast, simple, and accurate testing technique in photosynthesis research.

24-Epibrassinolide ($0.1\ mg \cdot L^{-1}$) could ameliorate the decrease in Pn and Fv/Fm caused by aluminum stress, indicating an enhancement in photosynthetic capacity (*14*). Under nickel stress, cadmium stress, and drought stress, exogenous BRs could also alleviate the decrease of leaf Pn and sustain higher photosynthetic metabolism level in plants (*5*, *15*, *16*). Huang reported that exogenous 24-epibrassinolide pretreatment on cucumber leaf could effectively alleviate the decrease of Fv/Fm under chilling stress (*17*). However, no significant effect of 24-epibrassinolide was observed on chlorophyll fluorescence in pepper under salt stress (*7*). Our results showed that weak light stress significantly reduced leaf Pn and Fv/Fm of two cultivars, and they decreased gradually with the extension of stress time, which was an injured performance of light-loving tomato under weak light. However, different concentrations of exogenous 24-epibrassinolide alleviated the decline of leaf Pn and Fv/Fm under weak light, which indicated that exogenous 24-epibrassinolide could protect the PSII reaction center from weak light stress to some extent, and maintained higher photochemical transformation efficiency and photosynthetic metabolism, thus improving plant tolerance to weak light stress. However, optimal induction concentrations were different between cultivars due to different resistance abilities to weak light.

Effects of Exogenous 24-Epibrassinolide on Plant Adaptability to Weak Light Stress. Due to weak light, leaf Pn and Fv/Fm decreased, but a series of adaptive responses could be started to decrease the injury and increase plant adaptability to weak light stress. In accordance with other research, weak light stress could obviously decrease leaf LSP, Amax, and Rd (*18−20*) and obviously increase chlorophyll, especially chlb content, but chla/chlb decreased (*21−23*); we obtained the same results in this experiment. The increase of chlb content is favorable for the increase of light-harvesting complex protein (LHCP) and the number of granum and granum lamella (*24*), as well as the harvesting of dominant short-wavelength blue violet light in diffused light, so as to increase the use of weak light. Moreover, the decrease of chla/chlb enhanced the reducing ability to 2,6-dichlorophenol indophenol in chloroplast, which improved the activity of photosynthetic phosphorylation. The decrease of leaf Rd could decline the consumption of assimilates, thereby keeping stable the accumulation of dry matter under the condition of decreased Pn due to weak light, so these changes were plant adaptive responses to weak light stress. In contrast, exogenous 24-epibrassinolide induced the further increase of chlb, the further decrease of chla/chlb, and the further decrease of Rd under weak light, which indicated that 24-epibrassinolide could induce the enhancement of plant adaptive response to weak light stress.

ABBREVIATIONS USED

IVF, Institute of Vegetables and Flowers; CAAS, Chinese Academy of Agricultural Sciences; BRs, brassinolides; Pn, net photosynthetic rate; Fo, initial fluorescence; Fm, maximum fluorescence; Fv/Fm, maximal photochemical quantum efficiency of PSII; PAR, photosynthetic active radiation; RH, relative humidity; chla, chlorophyll *a*; chlb, chlorophyll *b*; chl-(a+b), chlorophyll *a* and chlorophyll *b*; LSP, light saturation point; Rd, dark respiration rate; Amax, net photosynthetic rate at light saturation point; LHCP, light-harvesting complex protein.

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