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Research Article

Impacts of Brassinolide on the Photosynthetic Characteristics of ‘Qiyuexian’ Jujube

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Abstract: The jujube cultivar ‘Qiyuexian’ was chosen as object in this study. Effects of different concentrations of brassinolide (BL) on its characteristic parameters of light/CO_2 response curve were investigated. The results indicated that the mentioned parameters were significantly affected by the concentrations of BL. The Light Saturation Point (*LSP*) was significantly increased by 17.42% after being treated by 0.1 mg/L BL. After spraying 0.2 mg/L BL, the maximum net photosynthetic rate (P_{nmax}), apparent quantum efficiency (*AQY*), *LSP*, maximum carboxylation rate (V_{cmax}), maximum rate of photosynthetic electron transport (J_{max}) and Triose Phosphate Utilization rate (*TPU*) were significantly increased by 21.14, 20.26, 21.95, 21.14, 20.26 and 21.95%, respectively. The *AQY*, *LCP*, *LSP*, V_{cmax} and J_{max} were significantly increased by 12.55, 60.75, 19.00, 20.96 and 20.06% respectively after being treated by 0.3 mg/L BL, while the *LCP* and *LSP* were significantly increased by 65.53% and 25.79% respectively after being treated by 0.4 mg/L BL. In conclusion, 0.2 mg/L BL treatment could significantly accelerate the overall photosynthetic ability of “Qiyuexian” jujube, promoting its accumulation of assimilative products, which is beneficial to increase the production and quality of jujube fruits.

Keywords: Brassinolide, leaf spraying, light/CO_2 response curves, photosynthetic parameters, qiyuexian jujube

INTRODUCTION

Jujube (*Zizyphus jujube*) is a native economic tree species in China. Jujube tree has favorable tolerance to environmental stresses and poor soil, while its fruit contains abundant sugar, amino acid, vitamin C and phenolic compounds (Guo *et al*., 2015; Wang *et al*., 2016), hence, exhibiting important economic and ecological benefits. After long-term cultivation, jujube had become one of important fruit species and it has the 3rd largest cultivated area and the 7th largest yield among the fruit productions in China. Though the managements of jujube plantations are simple according to its favorable adaptability, further reasonable cultivation methods are still needed to improve the economic values of jujube.

Photosynthesis is an important physiological process and one of the key factors affecting not only the yield, but also the quality, including the content of sugar, fragrance, weight and color of jujube fruits. Previous studies indicated that the plant growth regulator such as jasmonic acid and salicylic acid can effectively increase the photosynthetic ability of plants and thus promote the accumulation of dry matter (Chen *et al*., 1993; Xu *et al*., 2016). Among the regulators, Brassinosteroids (BRs) has been regarded as a kind of plant growth regulators with the highest biological activity to increase the plant photosynthetic efficiency. For examples, Sairam (1994) reported that Brassinolide (BL) significantly increases the development, contents of chlorophyll and leaf area of wheat leaves. Shu *et al*. (2016) indicated that 2, 4-epibrassinolide significantly increases the contents of chlorophyll a and the ratio of chlorophyll a/b of tomato leaves. The investigations of previous studies have demonstrated that BRs can increase the activities of photosynthetic enzymes and the expressions of related genes (Ali *et al*., 2008; Ogweno *et al*., 2008; Hayat *et al*., 2010; Zhao *et al*., 2017; Pociecha *et al*., 2017). Besides, BRs also exhibited positive impacts on the transfer of photosynthetic products (Wu *et al*., 2008). For its mentioned benefits and the ability to increase fruit-setting percentage (Ali *et al*., 2006), BRs might be used to increase the photosynthetic efficiency and to increase the yield and quality of jujube. However, most of existed studies focus on the application of BRs on the

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production of crops and vegetables, especially in the adverse circumstance (Divi and Krishna, 2009; Holá, 2011; Hu *et al*., 2013; Sharma *et al*., 2013; Wu *et al*., 2014). The effects of its applications in jujube cultivation are still not reported.

‘Qiyuexian’ is an extremely precocious jujube cultivar bred by Northwest A&F University of China and demonstrates high tolerance to cold, salt and poor soil. It also exhibits high fruit-setting percentage, favorable adaptability to dwarf dense planting and protected cultivation and high fruit quality for fresh-eating (Gao *et al*., 2013). In this study, ‘Qiyuexian’ was chosen as object, the impacts of different concentrations of BL spraying on its photosynthetic characteristics were detected. The results might be helpful for explaining BRs effects on the responses of jujube’s photosynthesis to light and CO_2 and for increasing the yield and fruit quality of this improved jujube variety.

MATERIALS AND METHODS

Materials and experimental design: The experiment was conducted at the jujube experimental station of Northwest A&F University, Qingjian, Shaanxi, China. The climate here was classified as temperate continental monsoon climate, with an annual average temperature of 10°C, an annual average precipitation of 450 mm and a frost-free period of 200 days. In the plantation of *Zizyphus jujube*cultivar ‘Qiyuexian’, 5 years old jujube tree were chosen for this study. BL was purchased from Chaoyang Institute of Biological Hormone, Chengdu, China. The soluble powder was firstly dissolved using warm distilled water (50-60°C) and then diluted to 0.1, 0.2, 0.3 and 0.4 mg/L solutions using distilled water.

At the middle April (leaf-expansion period of jujube), the crown of 12 jujube trees was sprayed using 0.1, 0.2, 0.3 and 0.4 mg/L BL solutions respectively, until water dropped from leaves (each treatment has 3 replications), while 3 trees were treated using fresh water as control. A protective belt was set around the experimental area. After spraying, all jujube trees were treated with usual field managements until the middle August (fruit swelling period).

Determination of indices and calculation: For the determinations, mature leaf at the south part of crown was chosen. From 8:00 to 11:30 a.m., the characteristic parameters of light response curve were determined using a Li-6400 portable gas exchange system (Li-Cor Inc., Lincoln, NE, USA). The Li-6400 illuminant (Li-6400-02B) was used for setting photosynthetically active radiation (*PAR*) with different light intensity: 2000, 1600, 1200, 1000, 800, 600, 400, 300, 200, 150, 100, 50, 20 and 0 μmol/m^2/s. The net photosynthetic rate at the different light intensities was determined. During the determination, the air flow velocity was maintained as 500 mL/min, the temperature was 30±3.1°C, the CO_2 concentration was 380 μmol/mol and the relative environmental moisture was 40-60%.

Subsequently, the light response curve was simulated by the non-rectangle hyperbola model suggested by Farquhar *et al*. (2001) Eq. (1). The maximum net photosynthetic rate (P_{nmax}), Light Compensation Point (*LCP*), Light Saturation Point (*LSP*) and dark respiratory rate (R_d) were calculated according to the methods suggested by Farquhar *et al*. (2001). In addition, the light response curve within weak light scope ($PAR \leq 200$ μmol/m^2/s) was analyzed by linear regression and the Apparent Quantum Yield (*AQY*) was calculated:

$$P_n = \frac{AQY\cdot PAR + P_{n\max} - \sqrt{\left(AQY\cdot PAR + P_{n\max}\right)^2 - 4AQY\cdot PAR\cdot K\cdot P_{n\max}}}{2K} - R_d \tag{1}$$

In which P_n was the net photosynthetic rate and K was the curvature factor of the light response curve.

The CO_2 mixing system of Li-6400 was used as the gas source for providing different CO_2 concentrations: 2000, 1800, 1600, 1400, 1200, 1000, 800, 600, 400, 300, 200, 150, 120, 90, 60, 30 μmol/m^2/s. The net photosynthetic rate corresponding to different intercellular CO_2 concentration (C_i) was determined. During the determination, the air flow velocity was maintained as 500 mL/min, while the temperature was 30±3.1°C, the light intensity was 1400 μmol/mol (Saturated light intensity) and the relative environmental moisture was 40-60%.

A photosynthetic biochemical model modified by Farquhar *et al*. (1980) and Sharkey *et al*. (2007) was used for the simulation of the CO_2 response curve (photosynthetic rate-C_i). The model was divided to 3 scopes:

- In low C_i conditions (<200 mol/mol), $P_n$was limited by Rubisco, the model was presented as Eq. (2):

$$P_n = V_{c\max}\left[\frac{C_i - \Gamma^*}{C_i + K_c\left(1 + \frac{O}{K_o}\right)}\right] - R_l \tag{2}$$

- Along with the increase in C_i (>300 mmol/mol), P_n was limited by the reproduction of RuBP, the model was presented as Eq. (3):

$$P_n = J\left[\frac{C_i - \Gamma^*}{4C_i + 8\Gamma^*}\right] - R_l \tag{3}$$

- Along with the continuous increase in C_i, P_n was limited by *TPU*, the model was presented as Eq. (4):

Table 1: Characteristic parameters of light response curves of 'Qiyuexian' jujube under different BL concentrations

BL Concentration mg/L	P_{nmax} μmol/m^2/s	*AQY* μmol/μmol	R_d μmol/m^2/s	*LCP* μmol/m^2/s	*LSP* μmol/m^2/s
0	22.70±1.00b	0.0701±0.0032b	1.97±0.04a	29.3±0.8b	442±10b
0.1	25.60±0.90ab	0.0742±0.0036b	2.65±0.39a	38.1±5.1ab	519±2a
0.2	27.50±0.90a	0.0843±0.0001a	3.07±0.00a	40.0±0.9ab	539±15a
0.3	25.55±0.35ab	0.0789±0.0017a	3.34±0.43a	47.1±1.4a	526±2a
0.4	24.55±0.65ab	0.0642±0.0009b	2.92±0.19a	48.5±3.7a	556±12a

P_{nmax}: Maximum net photosynthetic rate; *AQY*: Apparent Quantum Yield; R_d: Dark respiration rate; *LCP*: Light Compensation Point; *LSP*: Light Saturation Point; Duncan's test was used for the *post hoc* analysis ($p \leq 0.05$); Different letters in the same column indicated significant differences

Table 2: Characteristic parameters of CO_2 response curves of "Qiyuexian" jujube under different BL concentrations

BL Concentration mg/L	V_{cmax} μmol/m^2/s	J_{max} μmol/m^2/s	*TPU* μmol/m^2/s	R_l μmol/m^2/s	G_m μmol/m^2·s/Pa
0	167±6.5 c	151±5.0 c	12.8±0.75 b	3.67±0.070 a	1.00±0.045 a
0.1	190±9.0 bc	168±7.5 bc	13.1±0.05 b	3.70±0.235 a	1.23±0.245 a
0.2	257±8.5 a	197±7.5 a	15.9±0.30 a	4.63±0.235 a	1.06±0.135 a
0.3	202±8.0 b	187±8.5 ab	14.5±0.45 ab	4.00±0.250 a	1.43±0.365 a
0.4	183±9.0 bc	147±3.5 c	13.5±0.55 b	3.62±0.225 a	0.88±0.100 a

V_{cmax}: Maximum carboxylation rate allowed by ribulose 1·5-bisphosphate carboxylase/oxygenase (Rubisco); J_{max}: Maximum rate of photosynthetic electron transport (based on NADPH requirement); *TPU*: Triose phosphate utilization rate; R_l: Light respiration; G_m: Mesophyll conductance

$$P_n = 3TPU - R_l \tag{4}$$

where, P_{n} was the net photosynthetic rate, V_{cmax} was maximum carboxylation rate, C_i was intercellular CO_2 concentration, $G_{\text{m}}$was mesophyll conductance, Γ^* was the photosynthetic compensation point (the dark respiration under light was not included), K_{c} and K_{o} were the Michaelis-Menten constants of Rubisco to CO_2 and O_2, *O* was the CO_2 concentration in the chloroplast (210 mmol/mol), R_{l} was the dark respiratory rate under light, *J* was electron transport rate, J_{max} was the maximum electron transport rate and the *TPU* was the triose phosphates utilization rate.

All indices' values were calculated using SPSS 21.0 IBM software according to the methods suggested by Sharkey *et al*. (2007) and Farquhar *et al*. (1980, 2001).

Statistical analyses: The data was analyzed using IBM SPSS 21.0 software. One-Way Analysis of Variance (ANOVA) was employed for the significance analysis and the Duncan's test was used for the *post hoc* analyses ($p<0.05$).

RESULTS

Except for R_d, the BL treatments significantly affected the characteristic parameters of light response curve of Qiyuexian jujube (Table 1). Specifically, the *LSP* of jujube was significantly increased by 17.42% ($p<0.05$, the same below) under 0.1 mg/L BL treatment. The P_{nmax}, *AQY* and *LSP* were significantly increased by 21.95, 21.14 and 20.26% respectively under 0.2 mg/L BL treatment. The *AQY*, *LCP* and *LSP* were significantly increased by 12.55, 60.75 and 19.00% respectively under 0.3 mg/L BL treatment, while the *LCP* and *LSP* were significantly increased by 65.53 and 25.79% respectively under 0.4 mg/L BL treatment.

Relative to its effects on the characteristic parameters of light response curve, BL exhibited weaker effects on the CO_2 response parameters (Table 2). Only 0.2-0.3 mg/L BL treatments significantly affected V_{cmax}, J_{max} and *TPU* of jujube. Specifically, the V_{cmax}, J_{max} and *TPU* of jujube tree were significantly increased by 21.14, 20.26 and 21.95% respectively under 0.2 mg/L BL treatment, while the V_{cmax} and J_{max} were significantly increased by 20.96% and 20.06% respectively under 0.3 mg/L BL treatment.

Duncan's test was used for the*post hoc* analysis ($p \leq 0.05$). Different letters in the same column indicated significant differences.

DISCUSSION

According to the light/CO_2 response curves of plant photosynthesis, a variety of important photosynthetic parameters such as P_{nmax}, *AQY*, *LCP*, J_{max}, V_{cmax}, *TPU* and R_d can be calculated. That can accurately reflect the effects of environmental factors and physiological status of plant itself on the photosynthetic efficiency. Thus they recently received increasing attention in the investigations of plant photosynthetic characteristics.

Our studies revealed that at suitable concentration (0.2 mg/L), BL treatment could significant increase the P_{nmax} of jujube tree, similar to the findings of Hayat *et al*. (2010), Ahammed *et al*. (2013) and Holá (2011). Considering the V_{cmax} simultaneously exhibited a significant increase, it was speculated that BL might accelerate the CO_2 assimilation by increasing the activity of rubisco of leaf (Shu *et al*., 2016), subsequently increasing the production of photosynthate and the net photosynthetic rate. Previous studies also support this hypothesis. For example, Xia *et al*. (2009) indicated that EBL(?) participates in the translation and transcription during the synthetic processes of enzymes and, increases the expression abundance of relative gene. Li *et al*. (2015b) also stated that EBL accelerates the up regulation of large and small subunit gene (*rbcL* and *rbcS*) of rubisco, thus increasing its activity, especially the initial activity. Pociecha *et al*. (2017) reported that BRs significantly increases the activity of rubisco activase. The abovementioned effects of BRs would certainly increase the quantity and activity of rubisco and consequently accelerate the carboxylation rate.

In addition, the present results demonstrated that the *TPU* of jujube tree was increased after BL treatment. This indicated that BRs might also increase the P_{nmax} by promoting the transfer of photosynthate, accelerating the regeneration of ribulose-1, 5-bisphosphate (RuBP) and thus increasing the J_{max}. These effects might be resulted from the positive effects of BL on the enzymes related to RuBP regeneration. For example, Xia *et al*. (2009) reported that EBL significantly accelerate the expression of genes related to sedoheptulose-1, 7-bisphosphatase (SBPase) and fructose-1, 6-bisphosphatase (FBPase), which can consequently increase the synthetic rate of RuBP and the metabolic rate of hydrocarbons.

Furthermore, BL can increase the P_{nmax} of jujube tree by accelerating its light use efficiency. The results indicated that 0.2-0.3 mg/L BL treatments significantly increased the *AQY* of jujube, while all BL treatments (0.1-0.4 mg/L) significantly increased its *LSP*. These results were also supported by the findings of Li *et al*. (2015a) and Hu *et al*. (2013). These indicated that BL treatment could significantly increase the abilities of light absorbing, transforming and utilization under weak light conditions and it could increase the ability of jujube utilizing hard light. That might be due to the regulation of the synthesis and degradation of photosynthetic pigments by BL (Honnerová *et al*., 2010), consequently, affecting the absorbing and transforming processes of light. The investigations of Wu *et al*. (2014) and Wang *et al*. (2017) demonstrated that BRs significantly increases the chlorophyll fluorescence parameters (F_v/F_m, F_v/F_o, F_v'/F_m' and $\Phi PSII$ etc.) of *Solanum melongena* and *Cinnamonumcamphora*, similar to our results. However, BL treatment could simultaneously increase the *LCP* of jujube at high concentration (0.3-0.4 mg/L). This was in contrast to the investigation of Hu *et al*. (2013), in which BRs significantly decreases the *LCP* of pepper. This phenomenon might be mainly caused by the biological interspecific differences between plant species.

It was noticeable that any BL concentration did not affect the R_d, R_l and G_m of jujube, which were contrast to abovementioned literatures. This might be caused by the differences in the species and concentration of BRs used in experiments, the differences treating approaches and the interspecific differences among receiver plant species. In addition, the previous studies mainly detected the BRs' effects on plants under adverse conditions (high and low temperature, drought, heavy metals contamination, etc.). Thus in this study (under suitable conditions for jujube), the regulation of BL might be not found.

CONCLUSION

BL treatments significantly affected the light/CO_2 response of 'Qiyuexian' jujube. Specifically, the *LSP* of jujube was significantly increased after being treated by 0.1 mg/L BL. The P_{nmax}, *AQY*, *LSP*, V_{cmax}, J_{max} and *TPU* were significantly increased after being treated by 0.2 mg/L BL. The *AQY*, *LCP*, *LSP*, V_{cmax} and J_{max} were significantly increased after being treated by 0.3 mg/L BL, while the *LCP* and *LSP* were significantly increased after being treated by 0.4 mg/L BL. In summary, 0.2 mg/L BL treatment could significantly accelerate the overall photosynthetic ability of "Qiyuexian" jujube, promoting the accumulation of assimilative products. Hence, BL application is beneficial to increase the production and quality of jujube fruits.

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