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Low concentrations of glycine inhibit photorespiration and enhance the net rate of photosynthesis in *Caragana korshinskii*

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Abstract

The inhibition of photorespiration can be used to improve plant carbon fixation. In order to compare the effects of three photorespiration inhibitors [glycine, $NaHSO_3$, and isonicotinyl hydrazide (INH)], photosynthetic parameters of leaves sprayed respectively with these chemicals were examined and their inhibiting efficiency was evaluated in *Caragana korshinskii*. Our results showed that 5 mM glycine could reduce the photorespiratory rate (P_R) effectively, while the net photosynthetic rate (P_N), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) significantly increased. The ratio of electron flow for ribulose-1,5-bisphosphate (RuBP) carboxylation to RuBP oxygenation was elevated markedly. $NaHSO_3$ and INH could also suppress the P_R in some cases, whereas P_N was not improved. The glyoxylate content increased considerably after application of low concentrations of glycine. These results suggested that low concentrations of glycine could suppress photorespiration by feed-back inhibition of glyoxylate and enhance photosynthesis by regulating g_s, C_i, and the distribution of electron flow in *C. korshinskii*.

Additional key words: chlorophyll fluorescence; gas exchange; nonstomatal factor; positive correlation; stomatal factor.

Introduction

In the photosynthetic process, Rubisco (a bifunctional enzyme) catalyzes RuBP carboxylation and oxygenation (Sidhu *et al.* 2014). The $[CO_2]/[O_2]$ ratio and temperature jointly determine whether RuBP is carboxylated or oxygenated (Khan 2007). Under most conditions, the probability of Rubisco binding to O_2 is approximately half that of its probability of binding CO_2, meaning that every third molecule of RuBP is oxygenated (Bauwe *et al.* 2012). Therefore, photorespiration consumes much of photosynthetic products (Bauwe *et al.* 2010). Meanwhile, photorespiration wastes ATP (Voss *et al.* 2013), reduces NADH/NADPH, and releases organic nitrogen (Hirel *et al.* 2007). These observations suggest that photorespiration is a wasteful metabolism in plants (Peterhansel and Maurino 2011). Consequently, it is possible that reducing photorespiration might be a primary mean for increasing photosynthesis and yields in plants (Peterhansel *et al.* 2013).

Although several studies have provided evidence for increasing photosynthesis and yield by spraying plants with the appropriate photorespiration inhibitors, effects of these inhibitors remain controversial. Bisulphite (HSO_3^-) has been found to react with glyoxylate to generate α-hydroxylsulphonates, which can inhibit the activity of glycolate oxidase (GO), a key photorespiratory enzyme, in order to block the oxygenation of glycolate (Zelitch 1957). It has been reported that P_N could be enhanced by treatment with low concentrations of bisulphite which suppresses P_R in wheat (Wang *et al.* 2000a), rice (Wang *et al.* 2000b), tea trees (Yang *et al.* 2008), strawberry plants (Guo *et al.* 2006), and cyanobacterium (Wang *et al.* 2003). However, the inhibiting effect of $NaHSO_3$ on photorespiratory process was not obvious in soybeans (Takenmoto and Noble 1982). INH could inhibit the activity of glycine decarboxylase (GDC) and subsequently

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Abbreviations: CE − carboxylation efficiency; Chl − chlorophyll; C_i − intercellular CO_2 concentration; F_0 − minimal fluorescence yield of the dark-adapted state; F_m − maximal fluorescence yield of the dark-adapted state; F_m' − maximal fluorescence yield of the light-adapted state; F_s − steady-state fluorescence yield; $\Delta F/F_m'$ − effective quantum yield of PSII photochemistry; FM − fresh mass; GDC − glycine decarboxylase; GGAT − glutamate:glyoxylate aminotransferase; GO − glycolate oxidase; g_s − stomatal conductance; INH − isonicotinyl hydrazide; J_c − electron flow to RuBP carboxylation; J_o − electron flow to RuBP oxygenation; J_T − total electron transport rate; P_N − net photosynthetic rate; P_R − photorespiratory rate; R_D − respiration rate; RuBP − ribulose-1,5-bisphosphate; SGAT − serine:glyoxylate aminotransferase; SHMT − serine hydroxymethyl transferase.

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block the glycolate oxidation in the photorespiratory pathway (Zelitch 1972). Wild and transgenic rice cultured in MS medium containing INH exhibited no photorespiratory activity (Hoshida *et al.* 2000). Similar to this, the photorespiration rate in *Reaumuria soongorica* has been found to be reduced by spraying the plant with INH (Bai *et al.* 2008). Glycine is an intermediate metabolite of photorespiratory process. During the photorespiratory metabolism, glutamate:glyoxylate aminotransferase (GGAT) and serine:glyoxylate aminotransferase (SGAT) catalyse the synthesis of glycine, which is the substrate of GDC. The glycine content of leaves is generally considered to be a sensitive indicator for alterations in photorespiratory carbon flow (Eisenhut *et al.* 2007). Glycine accumulation leads to an increase in certain photorespiratory intermediates, such as glyoxylate, which can feed back onto Rubisco (Häusler *et al.* 1996) and change the stoichiometry between electron transport and carbon assimilation (Leegood *et al.* 1995).

Caragana korshinskii Kom. (Fabraceae), a dominant shrub species in arid and semiarid areas, is widespread in the wilderness of western and northern China (Fang *et al.* 2011, Xu *et al.* 2012). The plant is very tolerant to drought, cold, salt, and other abiotic stresses (Yang *et al.* 2014) and plays an important role in holding sand, improving the soil, and serving as supplemental livestock forage in the Loess Plateau (Fang *et al.* 2008; Yan *et al.* 2012). However, a high P_R was found in the plants living in this area, which was caused by climatic features, such as intense sunlight, high temperature, and low humidity. In order to test the effects of three photorespiration inhibitors ($NaHSO_3$, INH, and glycine), the gas exchange, chlorophyll (Chl) fluorescence parameters, and glyoxylate content were measured to evaluate the effects on P_N, P_R, and electron transport rate in *C. korshinskii.*

Materials and methods

Plant growth conditions and treatments: Two-year-old *C. korshinskii* seedlings were grown in the Northwest A&F University experimental field in Yangling, Shaanxi. The experiment was conducted in August 2013. Three photorespiration inhibitors: glycine (5, 10, or 20 mM, *Amresco*, USA), $NaHSO_3$ (5, 10, or 20 mM, *Sigma*, USA), and INH (5, 10, or 20 mM, *Alfa*, USA) were respectively sprayed on the leaves of *C. korshinskii* at 06:00 h every day for 3 d prior to measurements. For every inhibitor, a total volume of 50 ml was sprayed on leaves of each plant. Each treatment was carried on three plants. Control plants were sprayed with water. All plants were well watered, and the moisture-holding capacity was appropriately maintained at 80%. Fresh *C. korshinskii* leaves of each plant were collected at noon on the day when measurement was carried out, and then stored in liquid nitrogen to determine glyoxylate and Chl contents.

Gas exchange and Chl *a* fluorescence measurements: Adult and healthy leaves were used for gas-exchange measurements using a portable photosynthesis system (*LI-6400XT*, *LI-COR*, *Lincoln*, Nebraska, USA) and Chl *a* fluorescence using a pulse-modulated fluorescence monitor system (*FMS-2*, *Hansatech*, UK). Parameters were monitored in all plants every two hours from 09:00 to 15:00 h on the day of the experiment. The measurements were replicated three times with one plant. P_N, C_i, and g_s were measured directly by portable photosynthesis system. Environmental conditions in chamber were kept for leaf temperature of 25–30°C, an ambient CO_2 concentration of 400–440 μmol mol^{-1}, and the relative humidity was maintained at 70%.

The same leaves were used to assay the Chl *a* fluorescence. Leaf samples were dark-adapted for 30 min. A low light [<0.1 μmol(photon) m^{-2} s^{-1}] was used to determine the minimal fluorescence yield of the dark-adapted state (F_0). In order to measure the maximal fluorescence yield of the dark-adapted state (F_m), a 0.8-s saturating pulse [5,000 μmol(photon) m^{-2} s^{-1}] was applied. A continuous illumination with actinic light [1,500 μmol(photon) m^{-2} s^{-1}] was used to assay the steady-state fluorescence yield (F_s) and maximal fluorescence yield of the light-adapted state (F_m'). Every plant was measured three times. Effective quantum yield of PSII photochemistry ($\Delta F/F_m'$) was calculated using the equation: $\Delta F/F_m' = (F_m' - F_s)/F_m'$ (Xu *et al.* 2012). Total electron transport rate (J_T) was calculated using the equation: $J_T = \Delta F/F_m' \times PPFD \times 0.5 \times 0.84$ (Fang *et al.* 2011, Yan *et al.* 2012). The respiration rate (R_D) was calculated using the equation: $R_D = R_N \times Q_{10}^{(Td-Tn)/10}$ (with $Q_{10} = 2.2$, Td was the leaf temperature; Tn was leaf temperature at dawn, R_N was respiratory rate) (Bai *et al.* 2008). The electron flow to RuBP carboxylation (J_c) was calculated using the equation: $J_c = 1/3\ [J_T + 8 \times (P_N + R_D)]$. The electron flow to RuBP oxygenation (J_o) was calculated using the equation: $J_o = 2/3\ [J_T - 4 \times (P_N + R_D)]$. P_R was calculated using the equation: $P_R = 1/12\ [J_T - 4 \times (P_N + R_D)]$ (Guan *et al.* 2004a).

Glyoxylate content: Glyoxylate was extracted and measured as described by Fahnenstich *et al.* (2008). Leaf material (100 mg) was homogenized in 1 ml of 100 mM HCl and 0.1% phenylhydrazine. The extracts were incubated 80°C for 5 min, then chilled on ice for 10 min and centrifuged at 10,000 × *g* for 2 min. The 200 μl of the supernatant was mixed with 750 μl of 18.5% HCl and 50 μl of 4% (w/v) $K_3Fe(CN)_6$. The mixture was centrifuged at 10,000 × *g* for 2 min and the absorbance of the supernatant was measured by a spectrophotometer at 520 nm (*V-1100D, MAPADA,* China) exactly 8 min after the addition of $K_3Fe(CN)_6$. As a control, $K_3Fe(CN)_6$ was omitted. Absorbance values were quantified using a standard curve generated from known concentrations of glyoxylate. Glyoxylate content was expressed as mmol glyoxylate per gram of fresh mass of the sample.

Chl content assay: Chl content was assayed according to the method of Huang *et al.* (2015) with a few modifications. Fresh leaves of 0.1 g were ground with cold 80% acetone solution. All manipulations were performed in dark environment. The absorbance was measured at 665 nm and 649 nm (spectrophotometer, *V-1100D*, *MAPADA*, China). The calculation of Chl *a* and Chl *b* contents [mg g^{-1}(FM)] was done based on the following equations:

$$\text{Chl } a = \left[\left(13.95\,\text{A}_{665} - 6.88\,\text{A}_{649}\right)\times \text{V}\right]/\left(1000\times \text{W}\right)$$

$$\text{Chl } b = \left[\left(24.96\,\text{A}_{649} - 7.32\,\text{A}_{665}\right)\times \text{V}\right]/\left(1000\times \text{W}\right)$$

where A_λ was the absorbance at the specific wavelength, V was the volume of the extracted liquid, and W was the fresh mass of the sample.

Statistical analysis: All data were calculated in *MS Excel* (version *2003*). Significance and correlation analysis were performed using *SPSS* for *Windows* (version *17.0*). One-way analysis of variance (*ANOVA*) method (LSD model) was used to detect the significance ($P<0.05$). Data were presented as the means ± SD. All figures were drawn using *Origin 9.1*.

Results

The effects of photorespiration inhibitors on P_R and P_N: The P_R of *C. korshinskii* decreased after all the treatments with glycine, $NaHSO_3$, and INH (Fig. 1*A–C*). Notably, after the treatment with 5 mM glycine, P_R significantly decreased by 48.0, 25.5, 22.0, and 31.3% at 09:00, 11:00, 13:00, and 15:00 h, respectively (Fig. 1*A*). P_N increased from 11.19 to 17.04 μmol(CO_2) m^{-2} s^{-1} at 9:00 h, 10.65 to 13.36 μmol(CO_2) m^{-2} s^{-1} at 11:00 h, 4.98 to 10.67 μmol (CO_2) m^{-2} s^{-1} at 13:00 h, and from 4.14 to8.38 μmol(CO_2) m^{-2} s^{-1} at 15:00 h after the treatment with 5 mM glycine, respectively (Fig. 1*D*). The 5 mM $NaHSO_3$ treatment effectively suppressed P_R at 09:00 and 13:00 h (Fig. 1*B*), but P_N did not raise (Fig. 1*E*). For INH treatments, both P_N and P_R were not influenced significantly except for 20 mM INH at 9:00 h. In addition, the P_N diurnally decreased in all treatments. A comprehensive evaluation of the effect of different treatments on photosynthesis and photorespiratory process is shown in Fig. 2. It is obvious that all inhibitor treatments could depress P_R. Glycine (5 mM) was the most effective in inhibiting photorespiration. Both

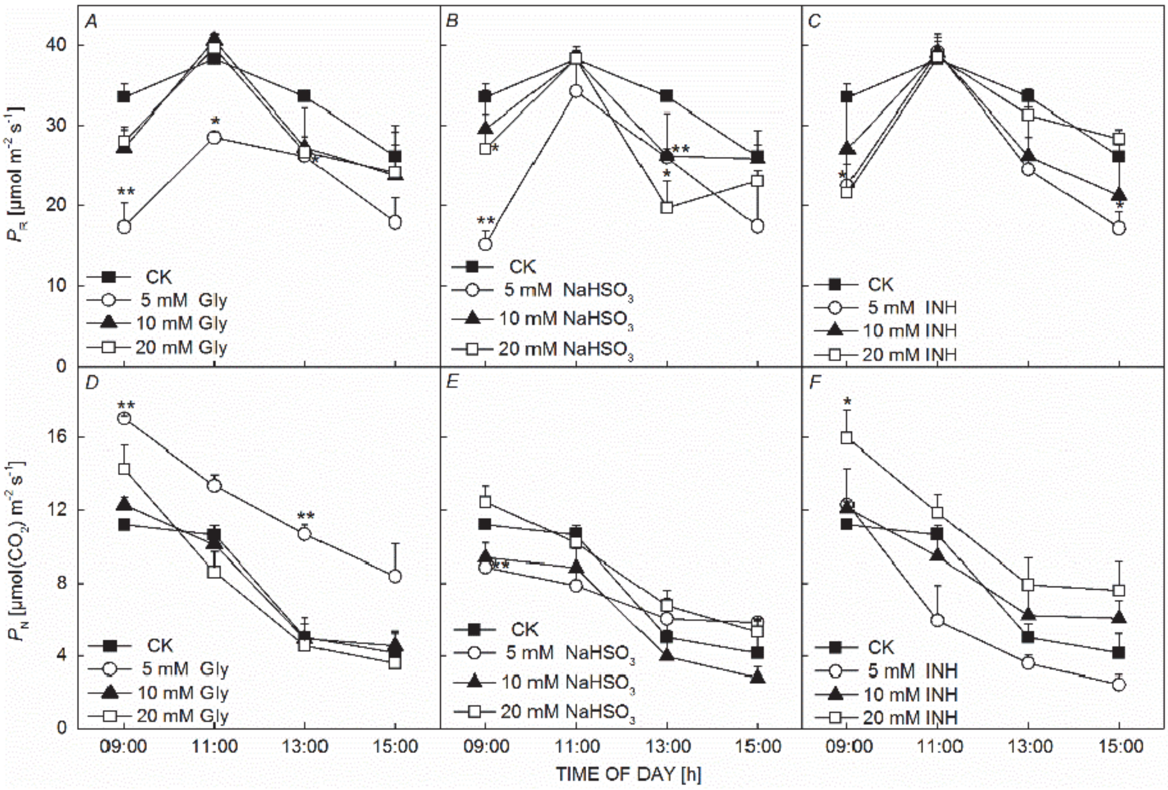

Fig. 1. The effects of various concentrations of glycine (*A*), $NaHSO_3$ (*B*), and isonicotinyl hydrazide (INH) (*C*) on photorespiratory rate (P_R) and of various concentrations of glycine (*D*), $NaHSO_3$ (*E*), and INH (*F*) on net photosynthetic rate (P_N) in *Caragana korshinskii* at different times during a day. The values represent means ± SD (*n* = 9). Significant differences between the treatments and the control are indicated using asterisks (*$P<0.05$, **$P<0.01$).

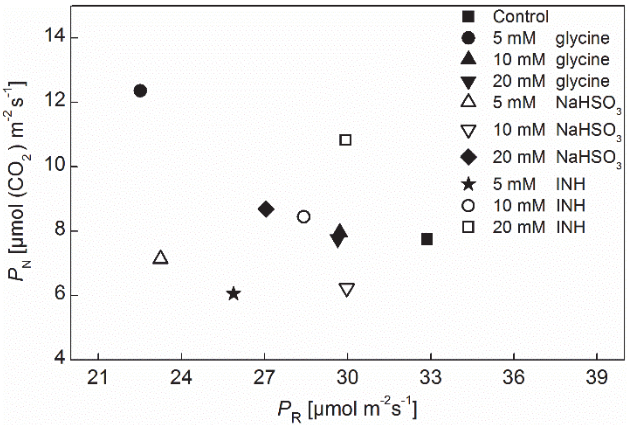

Fig. 2. Comprehensive evaluation of various concentrations of glycine, $NaHSO_3$, and isonicotinyl hydrazide (INH) on photorespiratory rate (P_R) and net photosynthetic rate (P_N). The values represent means. The optimal treatments located in *upper left* show the highest P_N and lowest P_R.

5 mM glycine and 20 mM INH could enhance P_N effectively. Taken together, 5 mM glycine was the optimal treatment for reducing P_R and improving P_N in all treatments (Fig. 2).

The effects of photorespiration inhibitors on g_s and C_i: It was found that g_s progressively decreased during the day time, but this pattern depended on each treatment (Fig. 3*A*,*B*,*C*). g_s progressively declined from 0.11 at 9:00 h to 0.05 mol(H_2O) m^{-2} s^{-1} at 15:00 h in control, C_i changed from 227.17 to 181.2 μmol(CO_2) mol^{-1}. When 5 mM glycine was applied, g_s fluctuated from 0.18 mol (H_2O) m^{-2} s^{-1} at 9:00 h to 0.09 mol (H_2O) m^{-2} s^{-1} at 15:00 h, while C_i changed from 284.03 μmol (CO_2) mol^{-1} to 225.84 μmol (CO_2) mol^{-1} (Fig. 3*A*,*D*). The 10 mM and 20 mM glycine treatments did not markedly affect g_s and C_i (Fig. 3*A*,*D*). All of $NaHSO_3$ treatments did not alter g_s and C_i except the increase of C_i with 5 mM $NaHSO_3$ at 15:00 h (Fig. 3*B*,*E*). g_s declined obviously with 5 mM INH at 11:00 h (Fig. 3*C*). C_i rose significantly with 10 mM and 20 mM INH at 13:00 h (Fig. 3*F*). Taken as a whole, g_s and C_i showed the similar inhibition effects, especially, with 5 mM glycine. A positive correlation was found between C_i and P_N (Fig. 4). These results suggested that 5 mM glycine could effectively enhance g_s and C_i, and then lead to the elevation of P_N.

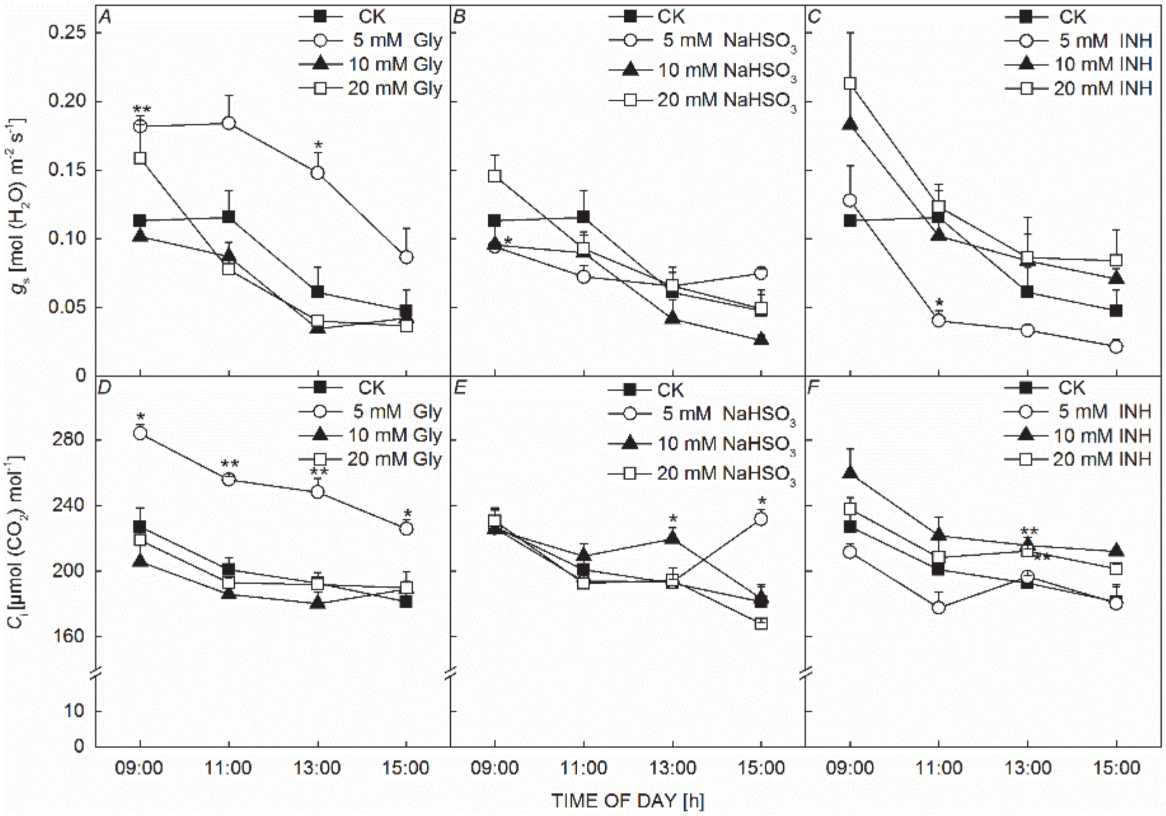

Fig. 3. The effects of various concentrations of glycine (*A*), $NaHSO_3$ (*B*), and isonicotinyl hydrazide (INH) (*C*) on stomatal conductance (g_s) and of various concentrations of glycine (*D*), $NaHSO_3$ (*E*), and INH (*F*) on intercellular CO_2 concentration (C_i) in *Caragana korshinskii* at different times during the day. The values shown represent means ± SD (n = 9). Significant differences between the treatments and the control are indicated by asterisks ($*P<0.05$, $**P<0.01$).

The effects of photorespiration inhibitors on J_c/J_T and J_c/J_o: The value J_c/J_T is an indication of the conversion of electron energy to active chemical energy. It was obvious that 5 mM glycine could elevate the value every time, and the most significant effect was found at 9:00 and 13:00 h (Fig. 5*A*), while 10 mM and 20 mM glycine markedly increased J_c/J_T at 9:00 h (Fig. 5*A*). The value of J_c/J_T rose significantly with 5 mM $NaHSO_3$ at 09:00 h and 20 mM $NaHSO_3$ at 13:00 h (Fig. 5*B*), as well as with 20 mM INH at 9:00 h (Fig. 5*C*). Correspondingly, 5 mM glycine could increase the value of J_c/J_o significantly most of the time (Fig. 5*D*). The value of J_c/J_o was elevated after the 5 mM $NaHSO_3$ treatment at 09:00 h (Fig. 5*E*) and 20 mM $NaHSO_3$ treatment at 13:00 h (Fig. 5*E*). Our results suggested that the chemicals inhibited photorespiration, which led to a higher electron flow through the Calvin cycle; this influenced P_N and P_R, especially after 5mM glycine treatment. This observation was consistent with the changes observed for P_R and P_N.

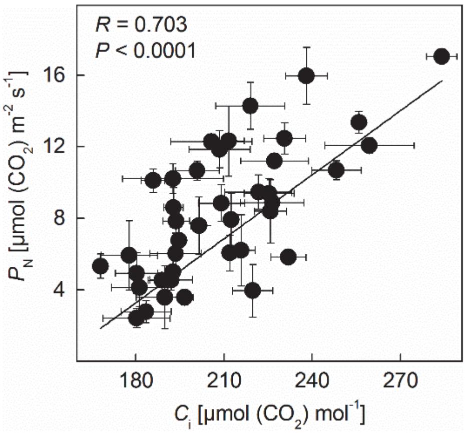

Fig. 4. The correlation analysis between intercellular CO_2 concentration (C_i) and net photosynthetic rate (P_N). All averages in different treatments at different times were shown. The values represent means ± SD.

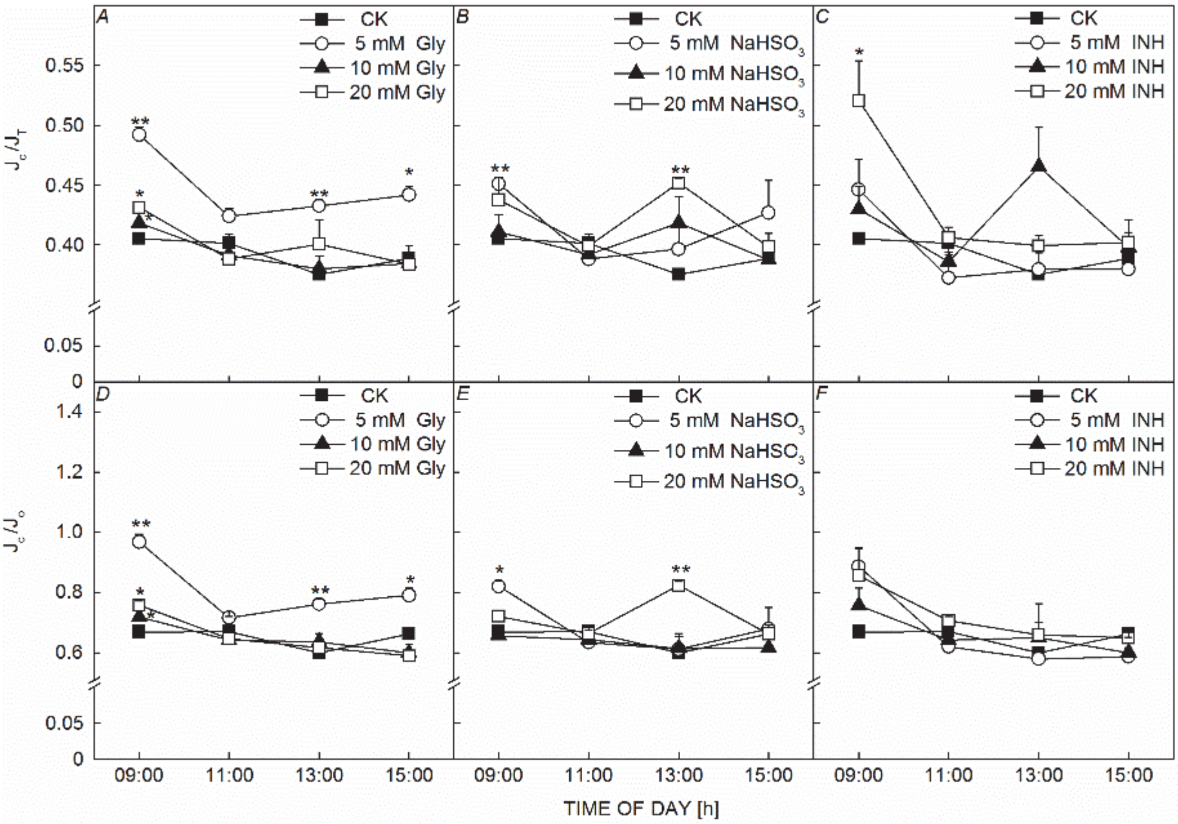

Fig. 5. The effects of various concentrations of glycine (*A*), $NaHSO_3$ (*B*), and isonicotinyl hydrazide (INH) (*C*) on the ratio of electron flow to RuBP carboxylation to total electron transport rate (J_c/J_T) and of various concentrations of glycine (*D*), $NaHSO_3$ (*E*), and INH (*F*) on the ratio of electron flow to RuBP carboxylation to electron flow to RuBP oxygenation (J_c/J_o) in *Caragana korshinskii* at different times. The values represent means ± SD ($n = 9$). Significant differences between the treatments and the control are indicated using asterisks (*$P<0.05$, **$P<0.01$).

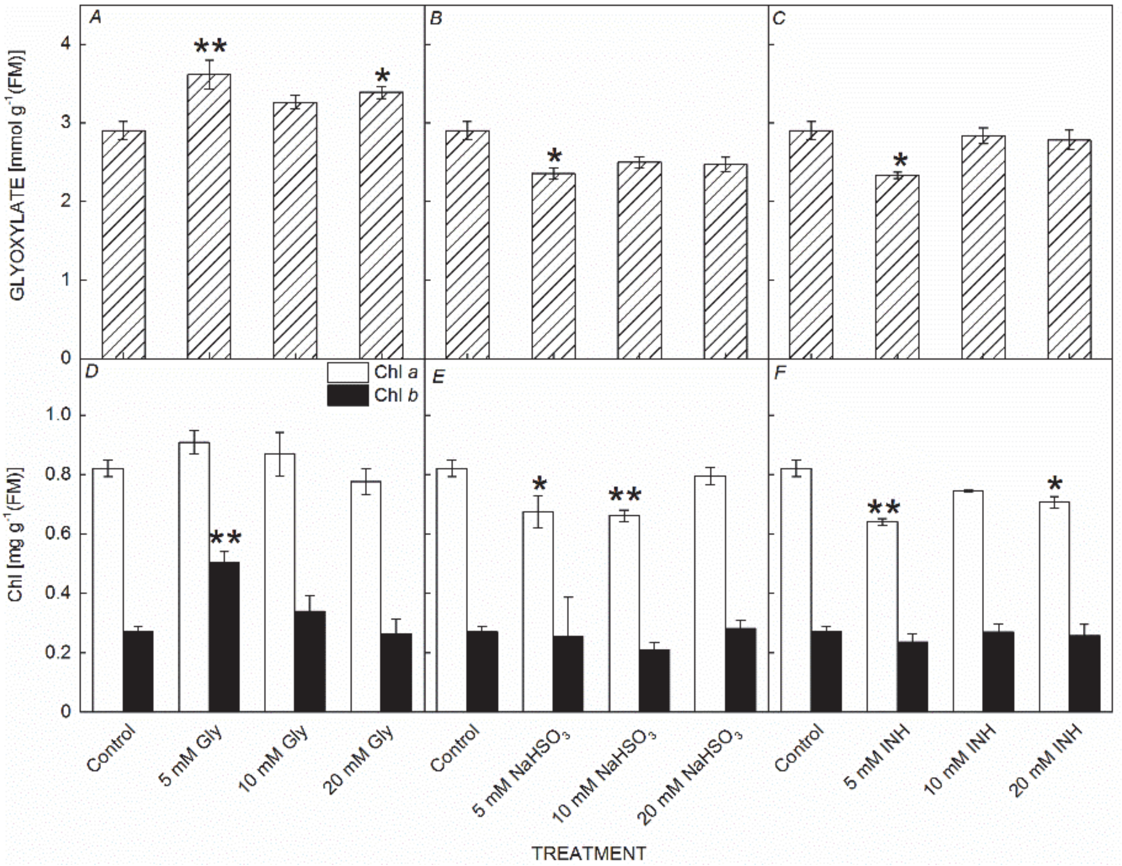

Fig. 6. The effects of various concentration of glycine (*A*), $NaHSO_3$ (*B*), and isonicotinyl hydrazide (INH) (*C*) on glyoxylate contents and of various concentrations of glycine (*D*), $NaHSO_3$ (*E*), and INH (*F*) on chlorophyll (Chl) *a* and Chl *b* contents in *Caragana korshinskii*. The values represent means ± SD ($n = 9$). Significant differences between the treatments and the control are indicated by different labels (*$P<0.05$, **$P<0.01$).

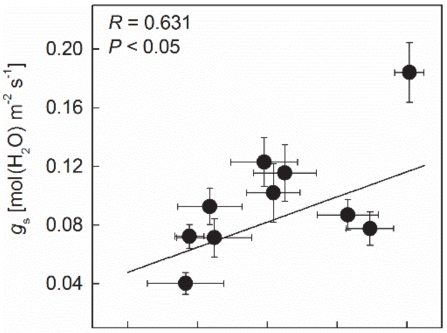

Fig. 7. The correlation analysis between glyoxylate content and stomatal conductance (g_s) in all treatments. The values shown represent means ± SD.

The effect of inhibitors of photorespiration on glyoxylate content: Glyoxylate is the major inter-metabolite in the photorespiratory process. The treatment with 5 mM glycine caused a significant increase in the glyoxylate content [from 2.9 to 3.61 mmol g^{-1}(FM) relative to the control] (Fig. 6*A*). No significant difference was found after the moderate and high glycine-concentration treatments (Fig. 6*A*). By contrast, $NaHSO_3$ and INH treatments induced a decline of the glyoxylate content relative to the control plants (Fig. 6*B*,*C*). The lowest glyoxylate value was found at 5 mM INH. Compared with the control plants, the glyoxylate content decreased by 18.9 and 19.6% after the treatments with low concentrations of $NaHSO_3$ and INH, respectively. In addition, a positive correlation was found between the glyoxylate content and g_s (Fig. 7).

The effects of photorespiration inhibitors on Chl content: The treatment with 5 mM glycine induced the increase of the Chl *b* content, while no difference was found in the Chl *a* content (Fig. 6*D*). However, $NaHSO_3$ and INH treatments resulted in a severe decrease of the Chl *a* content, especially, with 5 mM $NaHSO_3$, 10 mM $NaHSO_3$, 5 mM INH, and 20 mM INH. Such treatments, however, did not affect the content of Chl *b* (Fig. 6*E*,*F*).

Discussion

Reducing photorespiration by utilization of inhibitors might be an effective mean for enhancing photosynthesis in order to promote plant yields. Glycine, $NaHSO_3$, and INH are well-known photorespiration inhibitors. Glycine is an intermediate of the photorespiratory pathway, which could restrain photorespiration by feedback inhibition. In this study, photorespiration was inhibited by all glycine treatments. Especially, 5 mM glycine significantly decreased P_R and increased P_N. HSO_3^-could block photorespiration process by forming α-hydroxylsulphonates with glyoxylate to inhibit GO activity (Zelitch 1957). Numerous researches indicated that the application of $NaHSO_3$ to plants was shown to increase P_N in many species (Wang *et al.* 2003, Guo *et al.* 2006, Yang *et al.* 2008, Chen *et al.* 2014, Liu *et al.* 2015). In this experiment, all $NaHSO_3$ treatments depressed P_R. The greatest effect was found at 09:00 and 13:00 h with 5 mM $NaHSO_3$ (Fig. 1*B*). However, photosynthesis was not markedly enhanced (Fig. 1*E*). INH can block the glycolate oxygenation (Zelitch 1972) and the activity of GDC in the C_2 pathway (Naik 2006). It was reported that INH effectively inhibited photorespiration in *Reaumuria soongorica* (Bai *et al.* 2008), *Vitis vinifera* (Guan *et al.* 2004b), and rice (Hoshida *et al.* 2000). In the present study, 5 mM INH was observed to inhibit photorespiration in *C. korshinskii* at 09:00 and 15:00 h, whereas photosynthesis was not improved. Taken the effect on photorespiration and photosynthesis together, the low concentration of glycine was the optimal inhibitor in *C. korshinskii*.

Exogenous glycine might lead to an increase of glyoxylate by feedback inhibition. Glyoxylate is the precursor of oxalate biosynthesis, which can change the concentration of calcium ions in the plant by binding calcium and thus regulate the stomatal aperture (Sánchez-Martín *et al.* 2015). Therefore, low concentrations of glycine might increase the content of glyoxylate and decrease the concentration of intracellular calcium ions, thereby promote stomata opening in *C. korshinskii.* Correlation analysis of glyoxylate content and g_s also supported the hypothesis, resulting in more CO_2 transported into intercellular space *via* stomata.

Stomatal conductance regulates the diffusion of CO_2 and the transport of H_2O in plants, and thus influences photosynthesis. Previous research has suggested that C_i can be used to evaluate stomatal and nonstomatal factors affecting the values of P_N (Farquhar and Sharkey 1982). A decrease in P_N, which correlates to a decrease in C_i, is a consequence of stomatal factors, whereas a decrease in P_N, which correlates with an increase in C_i, may result from nonstomatal factors. Nonstomatal factors usually occurred when plants were subjected to stressful conditions. In the present study, both C_i and g_s were elevated significantly when the plants were treated with the low concentration of glycine compared with the control. Meanwhile, P_N and C_i presented a similar trend. Positive correlation between C_i and P_N also proved the increase of P_N resulted from the elevation of C_i. These results suggested that the increase in P_N resulted from stomatal factors under the condition of 5 mM glycine. In addition, CO_2 from glycine decarboxylation accounted for 75% of intercellular CO_2 (Kozaki and Takeba 1996), which could also explain the elevation of C_i with 5 mM glycine.

The increase of C_i enhances the local CO_2 concentration and the partial pressure of CO_2 near Rubisco. Ultimately, CE increased and the oxygenation of RuBP was restricted (Rivero *et al.* 2009). J_c/J_T indicates the relative importance of J_c. J_c/J_o is a good index of the relative rates of carboxylation *vs*. oxygenation (Silva *et al.* 2015). In the present study, of all the inhibitor treatments, the 5 mM glycine treatment exerted the strongest effect on J_c/J_T and J_c/J_o, which implied that more electrons flowed into RuBP carboxylation and that oxygenation was inhibited. The result correlated with the observed changes in P_N and P_R.

In summary, the effects of different chemicals on photorespiration and photosynthetic process were evaluated in this experiment. The results suggested that INH and $NaHSO_3$ could reduce P_R to some extent, but the effect on P_N was not obvious. Taken together, 5 mM glycine was the optimal inhibitor based on its effect on P_R and P_N. It might be because the low concentration of glycine promoted the accumulation of glyoxylate, which inhibited photorespiration, but also enhanced photosynthesis owing to regulation of g_s, C_i, and the distribution of electron flow for RuBP carboxylation and RuBP oxygenation in *C. korshinskii*.

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