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The Difference of Photosynthetic Responses to the Cadmium Stress Between a Wild Soybean (*Glycine soja* Sieb. et Zucc.) and a Cultivated Soybean

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Abstract The effects of Cd on a halophyte of Doingying wild soybean (DY-03262) were studied by comparing it with a cultivated soybean (SN-11) via investigating photosynthetic activity, chlorophyll fluorescence and Cd concentrations in leaves after treatment with different concentrations of Cd (0, 50, and 100 µM) for 10 days. There were no significant differences in photosynthetic rate (P_N), actual photochemical efficiency of PSII (Φ_{PSII}), stomatal conductance (g_s), and photochemical quenching (qP) between the both soybean species without Cd treatment, but they decreased greater in DY-03262 than that in SN-11 leaves after Cd treatment. The study demonstrated that the decrease in P_N were significantly correlated with Cd concentrations in the leaves of both soybeans species. The greater decreases in photosynthetic activity of the DY-03262 were due to the higher Cd concentrations in its leaves.

Keywords Bioaccumulation · Cadmium · Photosynthetic activity · Wild soybean

Soil contamination with heavy metals has become a critical environmental issue throughout the world. Cadmium (Cd), which is one heavy metal of concern in agricultural soils, stems mainly from livestock manures, atmospheric deposition, and fertilizers (Luo et al. 2009). Because of its high rates of soil-to-plant transfer, Cd can easily be taken up by crops and limits their growth and productivity, potentially affecting human heath after consumption (Satarug et al. 2010; Yuan et al. 2014; Zhong et al. 2015). Therefore, it is prudent to limit the entrance of harvest from Cd-contaminated agricultural soil into the human food chain. Many researchers have suggested that utilizing the Cd-contaminated agricultural soil to produce bio-energy, which will generates economic and environment benefits (Meers et al. 2010; Prasad 2015).

In this context soybeans, which are not only one of the most important crops in the human diet and animal feeds but also industrial products (Singh and Lee 2016), might be a sensible crop. However, previous studies have shown that the quality of soybean seeds and the agronomic traits of soybean plants are significantly affected on Cd-contaminated soils (Boggess et al. 1978; Ishikawa et al. 2005; Xue et al. 2014a; Zhou et al. 2013). Thus, it is important to develop soybean cultivars with increased Cd tolerance to increase yields when grown on Cd-contaminated soil. Wild soybean (*Glycine soja* Sieb. et Zucc.), the progenitor of soybean, have more genetic diversity than cultivated soybean (Zhou et al. 2015). What's more, there is no reproductive barrier between wild and cultivated soybean (Lam et al. 2010). Therefore, it has been adopted as a germplasm source for soybean breeding to improve resistance of cultivated soybean. Our previous studies demonstrated that halophyte of Dongying wild soybean (*Glycine soja* Sieb. et Zucc. ZYD 03262) can maintain higher photosynthetic activity under salt stress compared with cultivated soybean, which could be attributed to a mechanism that maintain low shoot Na^+ concentration by accumulating it in the roots (Chen et al. 2013; Xue et al. 2014b). However, until now,

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it has not been clear if the wild soybean also has a stronger Cd resistance than the cultivated soybean.

It is well known that photosynthesis in higher plants is sensitive to Cd stress. Numerous studies have demonstrated that the decrease in photosynthetic rate might be a result of the reduced chlorophyll contents (Mobin and Khan 2007), the obstructed electron transport (Sigfridsson et al. 2004), as well as the perturbation of enzymatic process of Calvin Cycle (Dias et al. 2013; Krantev et al. 2008).

Thus, in this study, we compared the Cd tolerance between the Dongying wild soybean and a cultivated soybean to explore the influence of different Cd concentration on photosynthetic activity in the two soybeans species. The possible mechanisms of Cd resistance in the wild soybean were also discussed.

Materials and Methods

Dongying wild soybean (DY-03262) seeds were collected from the estuaries of the Yellow River in Kenli County in the Shandong Province of China. The cultivated soybean [*Glycine max* (L.) Merr. Shanning 11] (SN-11) was widely grown in Shandong Province of China. Because the seed coat of the wild soybean is very strong to prevent water from getting into the seed. The wild soybean seeds were soaked with concentrated sulphuric acid for 3 min to destroy the seed coat. Whereas, the cultivated soybean germinates easily without any limitation by the seed coat, we did not treat it with concentrated sulphuric acid. Both seeds were germinated on vermiculite. The plants were grown in a greenhouse (the average quantum irradiance at midday = 1200 µmol m^{-2} s^{-1}, the average day/night temperatures = 30/22°C, the humidity = 75%–90%). After 12 days, the unanimous seedlings were transplant to pots (40 cm in height and 25 cm in diameter) containing quartz sand, which does not contain any other soluble minerals. There was one plant in each pot. The plants were supplied daily with Hoagland solution to avoid any potential nutrient and drought stresses. The Hoagland solution contained: 5 mM $Ca(NO_3)_2{\cdot}4H_2O$, 5 mM KNO_3, 2 mM $MgSO4{\cdot}7H_2O$, 1 mM KH_2PO_4, 0.1 mM EDTA-Fe, 47 µM H_3BO_3, 1 µM $MnCl_2{\cdot}4H_2O$, 0.25 µM $CuSO_4{\cdot}5H_2O$, 1 µM $ZnSO_4{\cdot}7H_2O$, and 0.01 µM H_2MoO_4. The treatment solutions were prepared with $Cd(NO_3)_2{\cdot}4H_2O$ to give Cd concentrations of 0, 50, 100 µM, approximately 0, 5.62 and 11.24 mg kg^{-1} in the soil. Although the exposure concentrations of Cd have not been confirmed by chemical analysis, the sand in the pot was flushed with sufficient treatment solution (about double amount of the water that the sand in the pot can hold) daily and extra solution leaked through a hole in the bottom of each pot. Therefore, the Cd levels would maintain a consistent as our setting concentration during the whole period of the experiment. The treatments were started at 20 days after transferring the seedling to pots. There were eight replicates for each treatment. The treatments continued for 10 days.

Three plants per treatment were randomly collected at the termination of the experiment to determine the length of shoots and roots. Then, the shoots and roots were weighed for the dry weight after drying at 80°C to a constant mass, when the difference value between the last two weighing less than 0.1% of the final weight.

The photosynthetic rate (P_N), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) were measured by a CIRAS-2 portable photosynthesis system (PP Systems, USA), connected with a PLC6(U) leaf cuvette. During each measurement, the photosynthetic photon flux density was maintained at 1200 µmol m^{-2} s^{-1}, temperature at 25°C and CO_2 concentration at 360 mmol mol^{-1} in the leaf cuvette. The light was provided by a red and blue LED source. Four replicate measurements were made for each treatment, and the results were averaged.

Chlorophyll fluorescence was measured using a FMS-2 pulse-modulated fluorimeter (Hansatech, UK). A 0.8 s saturating light of 8000 µmol m^{-2} s^{-1} was used for the dark-adapted (20 min) leaves to determine the maximal fluorescence (Fm). Then, the leaves were illuminated by actinic light at 1200 µmol m^{-2} s^{-1}. When the leaves reached steady-state photosynthesis, the steady-state fluorescence value (Fs) was recorded, and a second 0.8 s saturating light of 8000 µmol m^{-2} s^{-1} was used to determine the maximal fluorescence (Fm′) in the light-adapted state. Then, the actinic radiation was then turned off for 3 s, the minimal fluorescence in the light-adapted state (Fo′) was determined by illumination of 3 s far red light. The following parameters were calculated: (1) the actual photochemical efficiency of PSII, $\Phi_{PSII} = 1–Fs/Fm′$ (Genty et al. 1989); (2) the photochemical quenching, qP = (Fm′–Fs)/(Fm′–Fo′) (Baker 2008). Six replicate measurements were made for each treatment, and the results were averaged.

The Cd concentrations in the plants were determined using an atomic absorption spectrophotometer (AA6300, Shimadzu, Japan), equipped with deuterium lamp background correction and an air-acetylene flame. A Cd hollow-cathode lamp at a wavelength of 228.8 nm was used as a radiation source. The roots and leaves of the two soybean species for each treatment were separately harvested at the end of experiment, then rinsed with deionized water, dried to a constant mass at 80°C, and digested in concentrated nitric–perchloric acid (2:1, V/V). Three replicate measurements were made for each treatment, and the results were averaged.

Data were subjected to two-way analysis of variance (ANOVA), using SPSS 22, and were tested for homogeneity of variance with the Levene's test. Then multiple-comparison test of the means values was determined through least significant difference (LSD) test with a significance level of $p < 0.05$.

Results and Discussion

It has been proved that the shoot Cd concentrations varies not only among plant species (Li et al. 1997), but also among cultivars (Arao and Ae 2003; Florijn and Beusichem 1993; Ishikawa et al. 2005; Yan et al. 2010). Arao and Ae (2003) reported that Cd levels in soybean plants ranged from 0.46 to 2.7 mg kg^{-1} among 17 cultivars. Ishikawa et al. (2005) have suggested that the Cd concentrations in the shoot of younger soybean plant can be used to select low Cd-accumulation soybean cultivars. The Cd accumulation capacity of roots, which are the first organ to contact with Cd, determines the Cd concentrations in shoots (Sugiyama et al. 2007). Hydroponic experiments have shown that root morphological traits are closely related to Cd tolerance at young seedlings under different Cd treatments (0, 9, 23, 45, and 90 μM) (Wang et al. 2016). So Cd is strongly retained by plant roots and only a few fractions of the accumulated Cd can be transported to leaves (Cataldo et al. 1981), which was also confirmed by this study. The Cd concentrations in the roots of DY-03262 was much higher than that of SN-11 (Fig. 1a), and the Cd concentrations in DY-03262 leaves were 9.98 and 16.69 μg g^{-1} for 50 and 100 μM treatment (Fig. 2a), which was 1.21 and 1.72 times higher than that in SN-11. The ratio of Cd concentrations of the leaves to roots in DY-03262 was 0.021, 0.014 in plants with 50 and 100 μM treatment, respectively, and 0.031, 0.025 in SN-11 with the same treatments in this study, which indicates that the ratio of Cd concentrations of leaves to roots in DY-03262 was lower than that in SN-11. The accumulation of Cd in shoots of soybeans may be affected by Cd translocation from root to shoot (Sugiyama et al. 2007), so more Cd absorbed by the roots of DY-03262 might lead to more Cd translocated to the leaves.

It is known that the photosynthetic apparatus is particularly susceptible to Cd and the reduction of P_N is the common response in plants exposed to Cd stress (Andresen and Küpper 2013; Xue et al. 2014a). In this study, the P_N (Fig. 2a) and g_s (Fig. 2b) in leaves of the two soybean species decreased with increasing concentrations of Cd in the nutrient solution. Meanwhile, the decrease in DY-03262 leaves were significantly greater than that in SN-11 ($p < 0.05$). Compared with the changes of g_s and P_N, there were no significant changes of C_i in the leaves of the soybeans (Fig. 2), so the decrease of P_N was mainly caused by the damage of the mesophyll rather than the stomata. The results demonstrated that the different Cd treatments significantly decreased the dry weights of roots and shoots in both soybean species. The decrease in growth of the two soybean species after Cd treatments (Table 1) should be partly attributed to the significantly decreased P_N in leaves

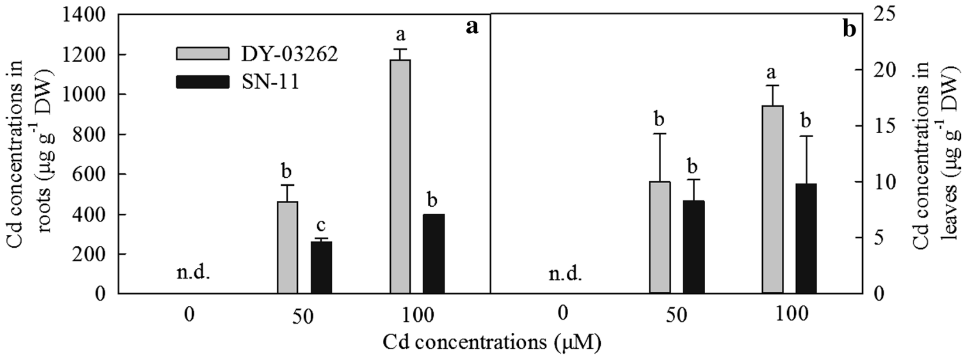

Fig. 1 The Cd concentrations in roots (**a**) and leaves (**b**) of DY-03262 and SN-11 after treated with different concentrations of Cd for 10 days. Values are the means ± SD (n = 3). The *different letters* present on top of *bars* indicate significant differences at $p < 0.05$

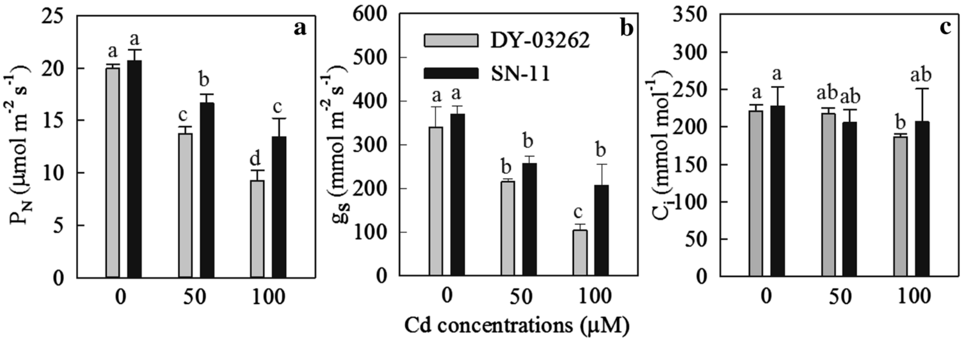

Fig. 2 The P_N (**a**), g_s (**b**), and C_i (**c**) in the leaves of DY-03262 and SN-11 after treated with different concentrations of Cd for 10 days. Values are the means ± SD (n = 4). The *different letters* present on top of *bars* indicate significant differences at $p < 0.05$

Table 1 Changes in root length, shoot length, root biomass, and shoot biomass of DY-03262 and SN-11 after treated with different concentrations of Cd for 10 days

Cd treatment (μM)	Root length (m)	Shoot length (m)	Root biomass (g)	Shoot biomass (g)
DY-03262				
0	0.21 ± 0.04a	0.96 ± 0.10a	1.93 ± 0.47b	3.43 ± 0.40ab
50	0.14 ± 0.02b	0.67 ± 0.11b	1.21 ± 0.39c	2.37 ± 0.62bc
100	0.10 ± 0.01cd	0.55 ± 0.04c	0.57 ± 0.12d	1.30 ± 0.19d
SN-11				
0	0.12 ± 0.01bc	0.19 ± 0.02d	2.91 ± 0.65a	4.10 ± 0.57a
50	0.09 ± 0.01d	0.16 ± 0.01d	1.68 ± 0.01bc	3.03 ± 0.24b
100	0.08 ± 0.01d	0.16 ± 0.01d	1.04 ± 0.10c	2.25 ± 0.37c

Data are the means ± SD (n = 3). The different letters present on the same column indicate significant differences at $p < 0.05$

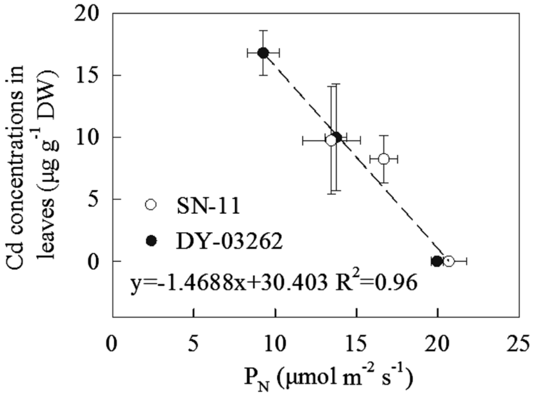

Fig. 3 Correlations between P_N and Cd concentrations in the leaves of DY-03262 and SN-11 after treated with different concentrations of Cd for 10 days (n = 6)

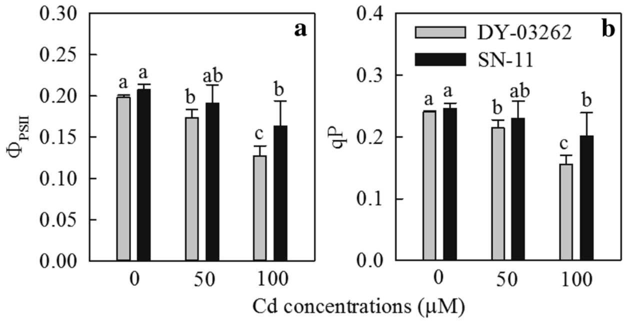

Fig. 4 The Φ_{PSII} (**a**) and qP (**b**) in the leaves of DY-03262 and SN-11 after treated with different concentrations of Cd for 10 days. Values are the means ± SD (n = 6). The *different letters* present on top of *bars* indicate significant differences at $p < 0.05$

($p < 0.05$). DY-03262 suffered a severer decrease in P_N than SN-11, and the root length, shoot length, root biomass, and shoot biomass of DY-03262 decreased by 51%, 43%, 70%, 62%, respectively under 100 μM Cd treatments, whereas, those of SN-11 decreased by 32%, 16%, 45%, 64%, respectively. These results indicate that DY-03262 is more sensitive to Cd stress than SN-11.

As shown in Fig. 3, the significantly correlation between the Cd concentrations and P_N in the leaves of both soybean species ($R^2 = 0.96$, $p < 0.01$) indicates that the P_N of the both soybean species has a similar response to Cd concentrations in leaves. The greater decrease of P_N in DY-03262 is mainly attributed to the higher concentrations of Cd in DY-03262 leaves compared to that in SN-11.

Many studies have shown that Cd in the leaves could interfere with the activation Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco, EC 4.1.1.39), which is the key enzyme involved in carbon assimilation. This influence could decrease the activity of Rubisco and damage its structure by substituting Mg^{2+} ions (Dias et al. 2013; Pietrini et al. 2003). The limitation of the CO_2 assimilation decreases the consumption of ATP and NADPH, leading to feedback inhibition of electron transport in chloroplasts. The inhibition of electron transport in chloroplasts is supported by the serious reduction in Φ_{PSII} (Fig. 4a) and qP (Fig. 4b) in leaves of both soybean species. Meanwhile, the remarkable reduction of Φ_{PSII} and qP in DY-03262 leaves compared with SN-11 indicates that less light energy was utilized by photochemical reaction and more excessive excited energy was produced in DY-03262 leaves. Although Cd is a non-redox metal that is unable to participate in Fenton and Haber–Weiss reactions, there are evidences that it can indirectly promote generation of reactive oxygen species (ROS) (Domínguez et al. 2010; Sandalio et al. 2001). The generation of ROS has potential to cause significant damage to membrane and other cellular structures, and inhibit plant growth (Andresen and Küpper 2013; Apel and Hirt 2004). Therefore, the more generation of ROS would cause the damage to membrane and the reduction of Rubisco contents (Romero-Puertas et al. 2002). The decrease of the P_N in leaves of the two soybean species with Cd treatments is partly due to the inhibition of Rubisco by the Cd (Dias et al. 2013; Pietrini et al. 2003).

So, compared with SN-11, the higher concentrations of Cd in DY-03262 leaves resulted in a greater decrease in P_N.

It have been demonstrated that the DY-03262 has an ability to accumulate higher levels of Na^+ in its roots, preventing the accumulation of higher concentrations of Na^+ in its leaves to protect the photosynthetic apparatus from salt damage (Xue et al. 2014b). Whereas, according to the results of this study, we conclude that the DY-03262 is not more resistant to Cd stress compared to the SN-11. This is because of the higher Cd concentrations in the DY-03262 leaves. Through the ratio of Cd concentrations of leaves to roots in the DY-03262 is lower than that in the SN-11, the higher Cd level in the DY-03262 roots leading to more Cd translocation to the leaves. Therefore, the greater decrease of P_N in DY-03262 is mainly attributed to the higher concentrations of Cd in DY-03262 leaves compared to that in SN-11. Then, we think that the mechanism of salt (NaCl) resistance in the DY-03262 is different from that of Cd resistance. It seems that the DY-03262 is not able to efflux Cd through the salt gland-like structures, which could secrete Na^+ to maintain lower Na^+ concentrations in leaves (Zhou and Zhao 2003).

However, why do the DY-03262 use different mechanisms to deal with different metal ions, and why are Cd ions not be secreted by the salt gland-like structures in leaves? To elucidate these questions needs further studies.

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