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Responses of pepper to waterlogging stress

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Abstract

One of the effective ways to address the effects of abnormal climate change on plant is to find germplasms that have better resistance to adverse environments. In this paper, we studied the responses of 5 pepper species *Capsicum annuum* L. (CA), *C. baccatum* L. (CB), *C. chinense* Jacquin. (CC), *C. frutescens* L. (CF) and *C. pubescens* Ruiz & Pavon (CP) as well as a wild pepper *C. baccatum* var. baccatum (CBY) to waterlogging stress. The results showed that warterlogging treatment greatly decreases photosynthetic pigment content, net photosynthetic rate (P_N) and stomatal conductance (g_s), and dramatically increases proline content and water-use efficiency (WUE) in all tested pepper, suggesting that pepper has weak resistance to waterlogging stress. The results also showed that changes of the above parameters vary in different species. CP had the smallest decreases in photosynthetic pigment content, P_N, and g_s and greatest increases in proline content and WUE. By contrast, CC had the greatest decreases in photosynthetic pigment content, P_N, and g_s and smallest increases in proline content and WUE, indicating that different species had different resistance to adverse environment and species CP and CC had the strongest and the weakest resistances, respectively. In addition, the study also demonstrated that wild pepper CBY had better resistance to adverse environment than all the tested species, indicating loss of the stress resistance genes during the process of domestication. Taking together, our study strongly suggests that pepper species should crossbreed with other species and wild pepper to expand genetic diversity, enlarge genetic distance, promote production, and improve the resistance to adverse environments.

Additional key words: pepper; warterlogging; resistance; species; crossbreeding.

Introduction

Increased human activities have significantly impacted global climate. Abnormal climate changes such as waterlogging caused by long-term rainfalls can affect plant growth and development. During waterlogging stress, plant photosynthesis and aerobic respiration are inhibited. Increased anaerobic respiration and hypoxia can result in an excessive accumulation of CO_2 and toxic compounds, leading to accelerated leaf senescence and abscission, increased stem diameter, aerenchyma formation, adventitious root production and so on. Study by Qu *et al*. (1999) on the effects of waterlogging on apple trees has found that short-term waterlogging can cause wavy arrangement of lower epidermis of young leaves and increase of leaf surface area, in favour of waterlogging tolerance and transpiration; by contrast, long-term waterlogging can cause disorganization of leaf epidermal cells and stomatal closure. Abbott *et al.* (1987) reported that leaves of waterlogged *Vaccinium corymbosum* have thinner epidermis, enlarged intracellular space in spongy tissues, and broken palisade tissues; while waterlogged *Vaccinium* spp. have thinner epidermis, enlarged intracellular space in spongy tissues, and relatively intact palisade tissue. Under waterlogging environment, flooded roots experience hypoxia as indicated by loss of root hairs and gradually elongated and blacked main root (Dong *et al.* 1997). However, under waterlogging stress, the roots of shallow-rooted hygrophytes are distributed on the soil surface, which is in favour of oxygen absorption,

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Abbreviations: CA – *Capsicum annuum* L.; CB – *Capsicum baccatum* L.; CBY – *Capsicum baccatum* var.baccatum; CC – *Capsicum chinense* Jacquin.; CF – *Capsicum frutescens* L.; CP – *Capsicum pubescens* Ruiz & Pavon; *E* – transpiration rate; FM – fresh mass; g_s – stomatal conductance; GR – glutathione reductase; P_N – net photosynthetic rate; SOD – superoxide dismutase; WUE – water-use efficiency.
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eventually leading to increased numbers of surface roots, thinner roots and root hairs (Zhao 2003, Andersen *et al.*1984). Wu *et al.* (1996) have shown that *Taxodium ascendens* grown on poorly drained soil has more and thinner horizontal roots and undeveloped root cavities, but no apparent main root. Setter *et al.* (2009) studied the waterlogging tolerance of wheat in Australia and India, and found that diverse element toxicities (or deficiencies) during waterlogging were proposed as a major reason why waterlogging tolerance at one site was often not replicated at another. Christianson *et al.* (2010) studied responses to waterlogging of cotton roots and leaves and found that waterlogging could result in significant reductions in stem elongation, shoot mass, root mass, and leaf number. Zheng *et al.* (2010) studied the effects of water stress of four provenances of neem (*Azadirachta indica* A. Juss) and the results indicated that provenance differences existed in the adaptation response to water stress that included changes to growth strategies coupled with ecophysiological and metabolic adjustments.

Pepper is classified to Solanaceae and originally planted in tropical areas of South America. It is a highly drought-tolerant vegetable, which contains the highest vitamin C content among vegetables, and has some medicinal value. International Board for Plant Genetic Resources (IBPGR) has classified pepper species into five species: *C. annuum* L., *C. baccatum* L., *C. chinense* Jacquin, *C. frutescens* L. and *C. pubescens* Ruiz & Pavon. Among them, *C. annuum* L. is the most differentiated, widely cultivated one and the focus in pepper breeding worldwide (Pickersgill 1997). Screening of waterlogging-resistant germplasms from drought-resistant cultivars is one of the important measures against abnormal climate changes. Studies on the resistance ability of pepper against waterlogging are few. Narrow genetic base of *C. annuum* (Prince *et al.* 1995) has greatly constrained the improvement of its yield and quality. Therefore, selecting waterlogging-resistant germplasms along with expanding genetic resources and increasing parental genetic diversities is the trend for pepper breeding. In this paper, a wild pepper and five species were used to study the characteristics of pepper under waterlogging stress and explore their responses to waterlogging stress by measuring their photosynthetic characteristics, enzyme activity, and leaf and root features. The study provides theoretical basis for cross-breeding and screening of waterlogging-resistant pepper species, expansion of genetic resources and improvement of pepper yield.

Materials and methods

Plants: Five pepper species, CA, CB, CC, CF, and CP, and wild CBY came from the United States Department of Agriculture and the Vegetable Institution of Hunan Academy of Agricultural Science. Each material was planted in 3 plots, at 50 plants per plot, and the plants were grown using the normal amounts of fertilizer and water.

Experimental design: During July to August, three healthy seedlings with similar growth conditions were selected from each of pepper species and wild pepper, and transplanted into a tub with diameter of 1 m. They were treated with regular water and fertilizer management in three replicates. During full blooming period, all peppers were over-irrigated to submerge their aerial parts of the seedlings for one, two and three consecutive days till one species shows severe wilt symptoms. This treatments were repeated and observed for three consecutive years.

Pigment analysis: Leaf samples were extracted in 95% acetone and measured spectrophotometrically (*Ruili UV-2100*, Beijing, China) at the wavelengths 663, 645, and 470 nm. Contents of chlorophyll (Chl) *a* and *b*, and carotenoids (Car) were calculated using the equations of Arnon (1949).

Gas exchange was determined between 09:00–11:00 h (Beijing time) in mid-August (heading stage) using *Li-6400* (*LICOR*, USA). P_N, g_s and E were measured at the irradiance of 1,000 μmol m^{-2} s^{-1}, temperature of 32±0.5°C, and the natural CO_2 concentration. WUE was calculated according to WUE = P_N/E.

Superoxide dismutase (SOD) measurement: 0.5 g of vein-free leaves were mixed with 2 cm^3 of 0.1 M phosphate buffer and ground on ice bath. Supernatant was obtained by centrifugation at 10,000 × *g* for 30 min, diluted to 10 cm^3 as crude enzyme and stored at 4°C for future use. 0.05 cm^3 of the crude enzyme was further diluted to 3.0 cm^3 with water containing 0.3 cm^3 of each 130 mM methionine, 0.75 mM nitrogen blue tetrazolium (NBT), 0.1 mM EDTA-Na_2 and 0.02 mM riboflavin and 1.5 cm^3 0.05 mM phosphate buffer. Enzyme was replaced with PBS buffer in control tubes. One control tube was set in the dark, the other control and the testing tubes were illuminated with 50 μmol m^{-2} s^{-1} fluorescent light for 20 min. Absorptions at 560 nm were measured by referencing to the absorption of the unilluminated control tube. Total and specific SOD activities were calculated based on the following equations: total SOD activity = (ACK – AE) × V/(0.5 × ACK × W × Vt), specific SOD activity = total SOD activity/protein content, where ACK was the absorption of illuminated control; AE was the absorption of tested samples; V was the total sample volume [cm^3]; Vt was the tested sample volume [cm^3]; W was fresh sample mass (FM) [g]; the unit of protein concentration was mg g^{-1}(FM).

Glutathione reductase (GR) activity was measured according to the method proposed by Gamble and Burke (1984). In detail, 0.2 g leaves were ground with 3 cm^3 extraction solution (0.1 M Tricine-NaOH buffer, pH 7.8, containing 2% PVP) at 4°C and centrifuged at 15,000 × *g* for 10 min. The obtained supernatant was diluted to 3 cm^3 as crude enzyme. Enzyme activity was measured in 1 cm^3 of the reaction solution containing 40 mM, Tricine-NaOH (pH 7.8), 0.5 mM GSSG and 0.1 mM NADPH. The reaction was initiated by addition of 0.2 cm^3 of the enzyme and recorded as a change of absorbance at 340 nm in 3 min. Control was similarly measured by replacement of GSS with water.

Proline determination: The fresh leaves were washed and dried with paper towel. After removal of rim and vein, about 0.5 g of leaves were cut into pieces, mixed with 5 cm^3 of 3% sulfosalicylic acid solution in a large tube, and boiled for 10 min under shaking. After cooling down, the extract was filtered with a funnel into a clean tube. 2 cm^3 of the filtered extract was mixed with 2 cm^3 of acetic acid and 2 cm^3 of acid ninhydrin, and boiled for 30 min after sealed with plastic wrap. After cooling down, 4 cm^3 of toluene were added into the tube and fully mixed. The upper red solution was collected and its absorption at 520 nm was measured using toluene as reference. Proline content (x) in the tested samples was obtained from the standard curve and the proline concentration in fresh leaves was calculated based on the following formula: proline content = (x × 5/2)/FM.

Determination of adventitious root number and root activity: The number of adventitious roots was measured directly. Root activity was measured by TTC method. In detail, roots were collected and washed. Their surfaces were dried carefully with absorbent papers. 0.5 g of root tip was selected, cut into 1-cm pieces, placed in a small beaker, incubated with 10 cm^3 1:1 (v/v) mixture of 1% TTC solution and 0.l M phosphate buffer (pH 7.0) at 37°C for 1 h in dark and then mixed with 2 cm^3 of l M sulfuric acid. Control was similarly performed except adding sulfuric acid first, root sample second, and the mixture last. The roots were then collected and ground with 3–5 cm^3 of ethylacetate and quartz sand in a mortar after removal of moisture to extract TTF. The remaining roots were further extracted with ethylacetate for 3 times. All the red extractions were collected, transferred into a new tube and diluted with ethylacetate to 10 cm^3. Absorption of the diluted extraction at 485 nm was measured. The blank solution was obtained similarly without adding root. Reduced TTC amount was obtained from the standard curve and its intensity in root tip was calculated as follows: TTC reduction intensity [mg g^{-1} h] = reduced TTC amount/FM h, Where FM was fresh root mass, and h is the incubation time.

Statistical analysis: Parametric data were analyzed using analysis of variance (*ANOVA*) in *Excel 2003*. Other data were analyzed using *t*-test. *P* values less than 0.05 and 0.01 were considered as statistically significant and highly significant, respectively.

Results

Photosynthetic pigments: Under normal conditions, the contents of photosynthetic pigments in the five species are different; they are the highest in CF, the lowest in CC and similar in the other three. Under waterlogging stress, the contents of photosynthetic pigments in all tested pepper species were decreased: CC had the biggest decrease (Chl *a*, Chl *b* and Car decreased by 68.3%, 64.3%, and 66.9%, respectively); CP had the second smallest decrease (Chl *a*, Chl *b* and Car decreased by 46.0%, 42.9%, and 50.1%, respectively); wild pepper CBY had the least decrease (Chl *a*, Chl *b*, and Car decreased by 31.2%, 32.6%, and 39.1%, respectively) (Table 1). Overall, the contents of photosynthetic pigments in pepper species decreased greatly, indicating that pepper species are not resistant to waterlogging stress.

***P*N**: Under normal conditions, P_N of all the tested species differed significantly (Fig. 1). CF had the greatest P_N of 21.77, CA had the second greatest of 17.73, and CP had the smallest of 15.78 μmol(CO_2) m^{-2} s^{-1}. P_N of wild

Table 1. Photosynthetic pigment content [g kg^{-1}(DM)] in different pepper species. Chl – chlorophyll. *Capital or lowercase letters* mean significance at 0.01 and 0.05 levels, respectively. Means of 9 replications ± SE.

Pepper species	Pigment content								
	Chl *a*			Chl *b*			Car		
	CK	W3	–%	CK	W3	–%	CK	W3	–%
CA	9.83 ± 0.58^{Bb}	4.03 ± 0.59^{Cb}	59.0	4.28 ± 0.12^{Bb}	2.35 ± 0.30^{Bb}	45.1	1.51 ± 0.11^{Aa}	0.49 ± 0.07^{Cb}	67.5
CB	9.31 ± 0.42^{Bb}	3.63 ± 0.21^{Cb}	61.0	4.45 ± 0.21^{Bb}	2.27 ± 0.14^{Cb}	49.0	1.19 ± 0.23^{Cb}	0.41 ± 0.04^{Cb}	65.5
CBY	9.51 ± 0.35^{Bb}	6.54 ± 0.20^{Aa}	31.2	4.23 ± 0.42^{Bb}	2.85 ± 0.11^{Aa}	32.6	1.28 ± 0.24^{Bb}	0.78 ± 0.10^{Aa}	39.1
CC	8.05 ± 0.78^{Bb}	2.55 ± 0.11^{Dc}	68.3	3.59 ± 0.25^{Cc}	1.28 ± 0.25^{Dc}	64.3	1.09 ± 0.10^{Cb}	0.36 ± 0.04^{Db}	66.9
CF	11.15 ± 1.00^{Aa}	4.71 ± 0.40^{Bb}	57.8	5.35 ± 0.53^{Aa}	2.46 ± 0.31^{Bb}	54.0	1.06 ± 0.08^{Cb}	0.46 ± 0.05^{Cb}	56.6
CP	11.15 ± 1.00^{Aa}	4.28 ± 0.15^{Bb}	46.0	3.87 ± 0.14^{Cc}	2.21 ± 0.14^{Cb}	42.9	1.12 ± 0.14^{Cb}	0.55 ± 0.01^{Bb}	50.1

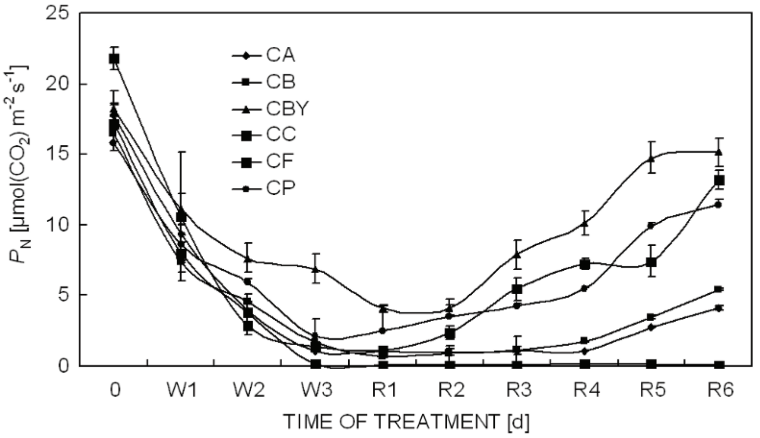

Fig. 1. Net photosynthetic rate (P_N) at 1,000 μmol m^{-2} s^{-1} of different pepper species. W1, W2, and W3 – plants treated with 1, 2, or 3-day waterlogging; R1, R2, R3, R4, R5 and R6 – plants treated with 1, 2, 3, 4, 5, or 6-day resumption of regular irrigation. Means of 9 replications ± SE.

Table 2. Stomatal conductance (g_s), transpiration rate (E) and water-use efficiency (WUE) of different pepper species. *Capital* or *lowercase letters* mean significance at 0.01 and 0.05 levels, respectively. CK – normally grown plants; W3 – plants treated with 3-day waterlogging. Means of 9 replications ± SE.

Pepper	g_s			E			WUE		
species	CK	W3	±%	CK	W3	±%	CK	W3	±%
CA	0.47 ± 0.08^{Bb}	0.06 ± 0.00^{Cb}	–87.2	3.26 ± 0.45^{Cb}	0.18 ± 0.09^{Dc}	–94.5	5.44 ± 0.75^{Bb}	6.06 ± 1.14^{Cb}	11.4
CB	0.43 ± 0.08^{Bb}	0.04 ± 0.00^{Cb}	–90.7	3.79 ± 0.26^{Ba}	0.30 ± 0.11^{Cb}	–92.1	4.35 ± 0.68^{Db}	5.47 ± 1.36^{Db}	25.7
CBY	0.44 ± 0.04^{Bb}	0.10 ± 0.01^{Aa}	–77.3	3.15 ± 0.48^{Db}	0.57 ± 0.23^{Aa}	–81.9	5.79 ± 1.09^{Bb}	12.07 ± 1.41^{Aa}	108.5
CC	0.43 ± 0.08^{Bb}	0.01 ± 0.00^{Dc}	–97.7	3.36 ± 0.49^{Cb}	0.17 ± 0.08^{Dc}	–94.9	5.11 ± 0.71^{Cb}	1.06 ± 0.33^{Ec}	–79.3
CF	0.55 ± 0.02^{Aa}	0.08 ± 0.01^{Bb}	–85.5	3.21 ± 0.47^{Db}	0.19 ± 0.08^{Dc}	–94.1	6.78 ± 1.21^{Aa}	7.42 ± 1.18^{Bb}	9.4
CP	0.34 ± 0.02^{Cc}	0.07 ± 0.01^{Bb}	–79.4	4.05 ± 0.58^{Aa}	0.39 ± 0.10^{Bb}	–90.4	3.89 ± 0.55^{Ec}	5.51 ± 1.13^{Db}	41.6

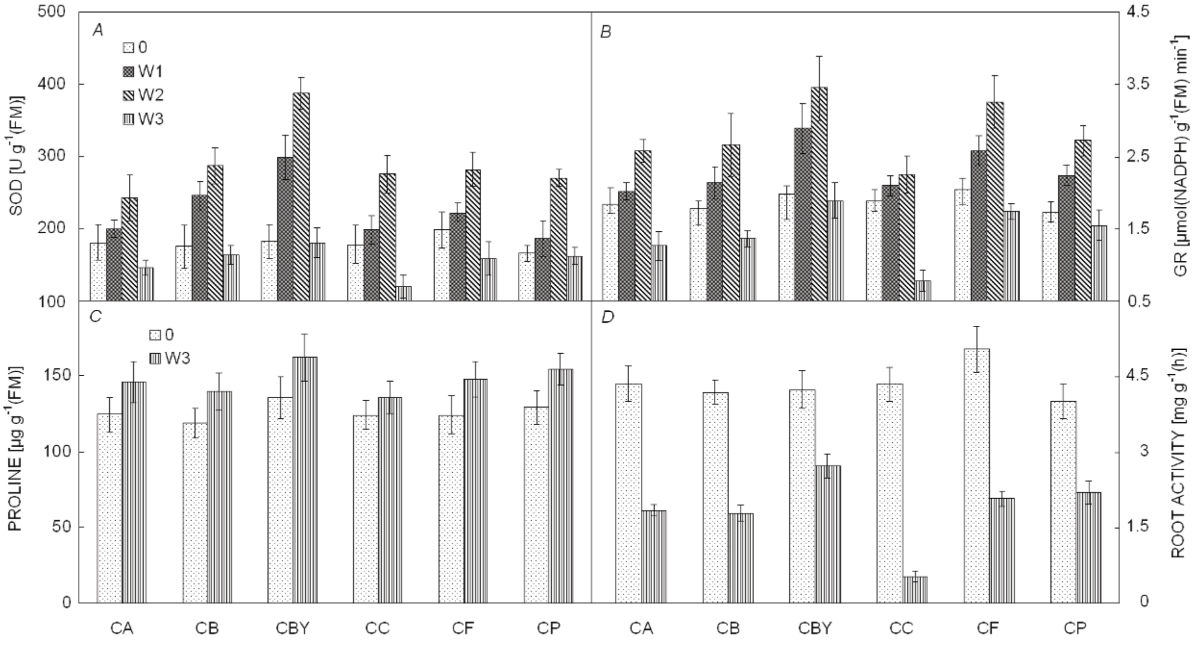

Fig. 2. Superoxide dismutase (SOD) activity (*A*), glutathione reductase (GR) activity (*B*), proline (*C*), and root activity (*D*) of different pepper species. W1, W2, and W3 – plants treated with 1, 2, or 3-day waterlogging. Means of 9 replications ± SE.

pepper CBY was smaller than that of CF, but higher than those of the other species. On the first day of waterlogging treatment, P_N of all the pepper species decreased and on the third day, P_N of CC was close to zero and that of CP and CBY was 2.15 and 6.88, respectively. P_N of all tested species continued declining on the first day of resumption of regular irrigation, but they started to increase on the second day, and almost recovered to the

Table 3. Number of adventitious roots of different pepper species. *,***t*-test significance at 0.01 and 0.05 levels, respectively. CK – normally grown plants; W3 – plants treated with 3-day waterlogging.

Plants	CA	CB	CBY	CC	CF	CP
CK	$23.23 \pm 3.21^{*}$	$24.25 \pm 2.10^{*}$	$30.36 \pm 4.76^{*}$	27.24 ± 4.58	$26.47 \pm 2.34^{*}$	$25.87 \pm 1.25^{*}$
W3	25.25 ± 3.98	26.58 ± 3.87	36.57 ± 2.47	$23.78 \pm 3.02^{**}$	28.25 ± 2.78	29.36 ± 2.14
±%	8.7%	9.6%	20.4%	–12.7%	6.7%	13.5%

normal level on the sixth day of the resumption except that of CC (Fig. 1). The results showed that CC had the least resistance to waterlogging; CP and CF had relative strong resistance. However, all their resistances were weaker than that of wild CBY.

g_s, *E*, and WUE: Three days after waterlogging treatment, stomata of all pepper species were closed. Their g_s was close to zero, indicating that stomatal limitation under waterlogging stress is an important reason for the decline in photosynthesis. In addition, WUE of all the tested pepper species was increased by different extents: CP and wild pepper CBY increased by larger ratio, which probably resulted in the greater resistance of the two pepper species to waterlogging (Table 2).

SOD and GR activity: Under waterlogging stress, the SOD and GR activities of all the pepper species first increased, reached to the highest at day 2, and then decreased (Fig. 2). On day two, SOD and GR activities of the CP increased by 125.62% and 221.13%, respectively. Those of wild pepper CBY increased by 212.39% and 174.24%, respectively, similar to those of CP. On day three, SOD and GR activities of the CC decreased by 32.71% and 58.51%, respectively; while CP decreased by 1.78% and 10.40%, respectively, and wild pepper CBY only decreased by 1.23% and 4.54%, respectively.

Proline and root activity: Proline contents increased under waterlogging stress by varying magnitudes among different species: that of CC only slightly increased, those of others increased by a larger proportion, wild pepper increased by 19.67% (Fig. 2*C*). By contrast, root activity significantly decreased: that was 87.61% in CC, 45.02% in CP and only 35.76% in wild pepper CBY (Fig. 2*D*).

Root number: Under waterlogging stress, the number of adventitious roots slightly increased in all other pepper except CC. The highest increase was 13.49% in CP among the five species, which was still smaller than that in wild pepper CBY (Table 3). These data indicated, on one hand, that pepper could maintain high oxygen diffusion rate and absorption efficiency by increasing the number of adventitious roots in order to reduce waterlogging caused oxygen stress; on the other hand, CP and the wild pepper had relatively strong resistance to waterlogging.

Discussion

Hypoxia caused by waterlogging can induce a series of responses in plants. One of the earliest responses is stomatal closure. Waterlogging does not induce water deficit in leaves and sometimes even improves leaf water potential in a relative long period. However, it can lead to stomatal closure in a short period and increase leaf resistance. Stomatal closure hinders CO_2 absorption, on the other hand, hypoxia induced by waterlogging inhibits synthesis of 8-amino-propyl acetate (5-ALA), the speed limit step of chlorophyll synthesis. Reduced CO_2-fixation ability of chloroplast and chemical changes of PSII system will lead to significant decrease in leaf photosynthetic rate (Beckman *et al.* 1992, Olien 1989). Our results showed that the photosynthetic rate and stomatal conductance of the five pepper species and wild pepper dramatically decreased under waterlogging condition and their recovery to normal levels after the drainage is lagged behind and needs time, indicating that pepper is not a good waterlogging-tolerant plant. This characteristic of pepper is probably because that pepper originates from tropical areas of Middle and North America. Under waterlogging condition, WUE increased significantly, indicating that pepper can avoid waterlogging stress by reducing water loss. In addition, photosynthetic rates of the various pepper species are different: CP and wild pepper CBY declined at relatively lower degree compared with those of the other species, indicating that CP and wild species have relative stronger resistance to waterlogging.

The adaptation process of crops to adverse environment is often accompanied by changes of some osmolytes. Studies have shown that under stress, plants are subjected to accumulation of proline in cells (Xing and Cai 1998). Proline accumulation can enhance resistance of plant to osmotic stress. Therefore, as an important cytoplasmic penetrant and antidehydrating agent, proline can reduce cell osmotic potential, improve the water-holding capacity of plant tissue and protect enzymes and membrane *in vivo* (Ma 1994). This study found that all tested pepper species have increased proline content under waterlogging stress, which proved the improvement of proline under stress condition is one of the selfdefense reactions of plants (Wu *et al.* 1997). Research has shown that stress-induced decrease of photosynthesis can lead to reduced demand for NADPH in Calvin cycle and consequently result in over-reduction of photosynthetic electron transport chain and disruption of photosynthetic electron transport, which eventually leads to the formation of reactive oxygen (Mittler *et al.* 2004). When plants accumulate reactive oxygen species (ROS), the contents of their endogenous ROS-scavenging enzymes also decrease (Fu *et al.* 2009, Jaeger *et al.* 2009) to a variable extent in different species (Liu *et al.* 2001, Ye *et al.* 2001). Our study showed that SOD and GR activities of all the tested pepper species are relatively high at the early period of waterlogging, but they decreased sharply after 3 days of the waterlogging treatment, resulting in the reduced ability to remove H_2O_2 and increased H_2O_2 accumulation, which further inhibit the activity of SOD and increase $O_2^{\cdot-}$ accumulation. In addition, H_2O_2 accumulation can also cause Harber-Weiss reaction to form more destructive ·OH, which directly leads to lipid peroxidation (Sun *et al.* 2005) and plant wilt and death. The declines of SOD and GR activities under waterlogging stress varied in different species: CC had the biggest decrease and CP had the smallest, indicating that the different species have different waterlogging resistance. Compared with wild pepper, the declines of SOD and GR activities in the five tested species were greater than those of the wild pepper, indicating the wild *C. annuum* has stronger resistance to waterlogging.

Taking together, our study found that wild pepper CBY had stronger resistant ability to waterlogging than all the tested species. Among the five tested species, CP had a higher photosynthetic rate and stronger resistance ability to waterlogging. The study suggests that pepper breeding should consider crossbreeding between species as well as between species and wild pepper, in one hand, to expand genetic source, increase genetic distance, and eventually increase production; on the other hand, to introduce elite stress tolerance genes and improve species' ability to resist adverse environments.

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