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PHYSIOLOGICAL AND PHOTOSYNTHESIS RESPONSE OF POPCORN INBRED SEEDLINGS TO WATERLOGGING STRESS

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Abstract

Waterlogging is one of the most severe global problems, which affects crop growth and yield worldwide, especially in the low-lying rainfed areas, and irrigated and heavy rainfall environment. Our objective was to study the physiological and photosynthetic characteristics of two popcorn genotypes under waterlogging conditions. The experiment was carried out in pots with two contrasting inbred lines differing in waterlogging tolerance: Q5 (tolerant) and Q10 (sensitive). Leaf gas exchange, oxidative stress, and chlorophyll (Chl) fluorescence were measured at 0, 2, 4, and 6d in the control and waterlogged plants. A decrease in net photosynthesis, stomatal conductance, and transpiration was observed in both genotypes. The waterlogging-sensitive plants showed reduced chlorophyll fluorescence, chlorophyll content and increased activity of peroxidase and polyphenol oxidase. Response curves for the relationship between photosynthetically active radiation (PAR) and net photosynthetic rate (P_N) for waterlogged plants were similar in both genotypes. The different physiological and photosynthetic response in the two popcorn inbred lines might be responsible for higher tolerance of Q5 than Q10. These results suggest that Q5 popcorn inbred lines are a source of genetic diversity for important traits such as P_N and WUE.

Key words: Popcorn, Waterlogging, Physiology, Photosynthsis, Chlorophyll content, Chlorophyll fluorescence.

Abbreviations: **AQY**-apparent quantum yield; **Chl**-chlorophyll; **E**-transpiration; $\mathbf{F_v/F_m}$-maximal quantum yield of PS II; $\mathbf{g_s}$-stomatal conductance; $\mathbf{L_s}$-light saturation point; $\mathbf{L_c}$-light compensation point; **PAR**-photosynthetically active radiation; $\mathbf{P_{max}}$-maximal photosynthetic rate; $\mathbf{P_N}$-net photosynthetic rate; **WUE**-water-use efficiency; $\mathbf{\Phi_{PS}}$ -effective quantum yield of PSII photochemistry.

Introduction

Waterlogging is a severe problem affecting crop growth and yield worldwide, especially in the low-lying rainfed areas, under-irrigated and heavy rainfall conditions (Altaf *et al*., 2015). The oxygen deficiency in rhizosphere restricts mineral nutrient and water uptake and alters plant metabolism, affecting the growth and development of plants (Crawford & Braendle, 1996). Waterlogging usually induces a rapid and significant reduction in the photosynthetic rate of many plant species (Pezeshki *et al*., 1996), particularly that of sensitive species. The reduced photosynthetic rate under waterlogging conditions is related to disruption in photosynthate transport (Sij & Swanson, 1973), stomatal conductance (Bradford, 1983), decline in leaf chlorophyll (Chl) content (Bradford, 1983). Chloroplasts were not only the location of the photosystems I (PSI) and II (PSII) and the site of photosynthesis, but also the major sites for generation of reactive oxygen species (ROS) such as hydrogen peroxide (H_2O_2) and superoxide anion radicals ($O_2^{\cdot-}$) during electron transport (Foyer *et al*., 1994, Asada, 1999). The accumulation of ROS in chloroplasts during photosynthesis further leads to oxidative damage to PSII under severe stress. Studies reported that ROS scavenging system including antioxidants such as superoxide dismutase (SOD), as corbate peroxidase (APX), catalase (CAT), and peroxidase (POD) minimize the cellular damage caused by ROS (Khatun *et al*., 2008; Fakhra *et al*., 2015). The antioxidant enzyme activities decrease along with increased ROS accumulation in plants under waterlogging stress (Ahmed *et al*., 2002; Lin *et al*., 2004; Jebara *et al*., 2005; Duan *et al*., 2008; Xie *et al*., 2008). Damaged PSII reduces the efficiency of photosynthetic electron transport, which results in substantive accumulation of ROS and further diminishes the photosynthesis of leaves under waterlogging stress. Increased ROS levels in plant leaves under waterlogging stress had been reported previously (Yan *et al*., 1996; Yordanova *et al*., 2004; Jamei *et al*., 2009). The increased levels of active oxygen stimulate cellular protective mechanism to attenuate the damage, with dramatically decreased SOD activity observed in corn (Yan *et al*., 1996). Yordanova *et al*. (2004) concluded that a significant increase in POD activity in leaves of *Hordeum vulgare* L. after 3 d of waterlogging, which was also observed in leaves of the flood-susceptible clone under flooded conditions (Bertolde *et al*., 2012). Polyphenol oxidases (PPOs) oxidize a broad group of phenols, with activity altered in some plants by abiotic stress (Sánchez *et al*., 2000). Malonaldehyde (MDA) was an important product of membrane lipid peroxidation. The content of MDA reflects the level of membrane lipid peroxidation (Guo *et al*., 2015).

Maize (*Zea mays* L.) is an important cereal crop. Popcorn seedlings, especially grown in low-lying rainfed areas, and irrigated and high rainfall conditions easily encounter waterlogging, resulting in substrate saturation and partial or complete seedling submergence. Popcorn seedlings capable of tolerating better waterlogging grow better than the sensitive inbred lines. The challenge is to combine physiological traits most effectively to produce waterlogging-tolerant or resistant germplasm. Therefore, evaluation of waterlogging conditions appears to be necessary to conserve tolerant genotypes. The aim of this work was to evaluate the tolerance and physiological responses of popcorn inbred line seedlings under waterlogging conditions.

Material and Methods

Plant material and experimental design: The experiment was conducted at the Research and Education Center of Agronomy, Shenyang Agricultural University. Two popcorn inbred lines were used including the tolerant Q5 and sensitive Q10. The popcorn seeds were planted in pots of 30cm height and 25cm diameter. The pots were randomly placed outdoors at the Research and Education Center of Agronomy. Each pot was filled with soil collected from the experimental field, where the popcorn was planted. Two treatments were designed: (1) control (CK), with pots irrigated every day, with water added and allowed to leak from the bottom; and (2) waterlogging (W), with the water level maintained about 10cm above the soil surface. Each treatment per genotype consisted of 30 pots (3 plants per pot). The fifth fully expanded leaves from the plant bottom were harvested to conduct all the physiological measurements at 0, 2, 4, and 6 days after waterlogging initiation.

Leaf gas exchange and Chl fluorescence: P_N, g_s and E were measured between 9:00h and 11:00h on the fifth fully expanded leaves of popcorn at 0, 2, 4, and 6 days after waterlogging using a Li-6400 portable photosynthesis system (LI-COR, Lincoln, NE, USA) equipped with an artificial irradiance source 6400-02B Red Blue. The measured light intensities were set to actual light intensities and the CO_2 partial pressure was set to 400μmol s^{-1}. Photosynthetic light responses were measured at 25ºC air temperature by an internal red and blue radiation source (LI6400-02). Fourteen irradiance levels (0, 20, 50, 100, 200, 400, 600, 800, 1000, 1200, 1400, 1600, 1800, and 2000μmol m^{-2} s^{-1}) were used. The air flux entering the cuvette was settled at 400μmol s^{-1}. Maize leaves were acclimated to each photosynthetic photon flux density (PPFD) for 4 min, andthe steady-state gas-exchange properties were logged, and the PPDF in the cuvete was changed. Light-response curves were plotted using the mean values of P_N measured at each PPFD. Light-response data were fitted to a model of nonrectangular hyperbola (Marshall & Biscoe, 1980) to estimate the apparent quantum efficiency (AQY), light compensation point (L_c), and light saturation point (L_s). The dark-adapted and light-adapted Chl flurescence was measured on the same fully expanded leaves using a pulse amplitude modulated leaf chamber fluorometer (LI-COR, Lincoln, NE, USA). Instantaneous water-use efficiency, WUE, was determined as the ratio of P_N to E (Sikder *et al*., 2015).

Chl content: Waterlogging usually reduces leaf Chl concentration. Leaves used for gas-exchange measurements were collected, immediately frozen on ice, and transported to the laboratory. The leaf samples were wiped, the edge and midrib removed, and 0.1 g leaf was cut and homogenized in a flask with 10 ml ethanol: acetone (1:1, v/v). The flasks were sealed with plastic wrap and placed in the dark. Leaf fragments were completely white after overnight extraction. The absorbance of the extracted liquid was recorded at 645nm and 663 nm against the miscible liquids (Wang, 2006). The Chl a, Chl b, and Chl a+b contents [mg g^{-1} (FM)] were calculated using the following equations (Arnon, 1949):

$$\text{Chl a} = [(12.7A_{663} - 2.69A_{645}) \times V] / (1000 \times W) \quad (1)$$
$$\text{Chl b} = [(22.9A_{645} - 4.68A_{663}) \times V] / (1000 \times W) \quad (2)$$
$$\text{Chl a+b} = \text{Chl a} + \text{Chl b} \quad (3)$$

where A_λ is the absorbance at wavelength λ nm, V is the volume of extracted liquid, W is the mass of sample.

Peroxidase and polyphenol oxidase activities: To analyze the activity of peroxidases (PODs; EC1.11.1.7) and polyphenol oxidases (PPOs, EC 1.10.3.1), samples were collected from the fifth fully expanded leaves from the bottom of plant at 0, 2, 4, and 6 d of control and waterlogged plants of both genotypes. Enzyme activities were determined using methodology similar to that described by Pirovani *et al*. (2008).

MDA content: MDA content was measured by the method of Wang (2006).

Statistical analysis: Mean comparisons were made using *t*-test ($p<0.05$) of SPSS 13.0 (SPSS, CHICAGO, USA).

Results

Photosynthetic pigments: Photosynthetic pigments following all treatments at the beginning 2 d of the experimental period were not significantly different ($p>0.05$) in both genotypes (Table 1). However, 4 days after waterlogging treatment, Chl a and Chl a+b were lower in the waterlogged plants compared with the controls in both genotypes. The Chl a and Chl a+b in waterlogging-tolerant genotype of Q5 were decreased less than in the waterlogging-sensitive genotype of Q10.

Photosynthetic characteristics: Significant decreases ($p<0.05$) in P_N, g_s, E and WUE were observed in both popcorn inbred lines (Table 2), after 4d and 2d of waterlogging in the tolerant (Q5) and sensitive (Q10) genotypes, respectively. Also, in the tolerant (Q5) genotypes P_N, g_s, E and WUE were about -46.45%,-29.41%, -37.59%, and -14.19% lower in waterlogged plants relative to controls after 6d. In the sensitive (Q10) genotype, P_N, g_s, E and WUE were about -58.97%, -61.11%, -44.92%, and -25.56% lower relative to controls after 6d of waterlogging, respectively. The P_N, g_s, E and WUE in the tolerant genotype of Q5 were decreased less than in the sensitive genotype after 6d of waterlogging, respectively.

Differences in homogeneity of slopes (Steel & Torrie, 1980) were only detected for response curves of P_N to increasing PAR of both genotypes. The PAR response curves displayed significant decline in P_N after 6d of waterlogging for both genotypes. The PAR response curve for P_N of Q5 was decreased less than that of the waterlogging-sensitive genotype (Fig. 1). The light saturation point (L_s) of tolerant Q5 was 1584μmol m^{-2} s^{-1} under CK and 996 μmol m^{-2} s^{-1} under waterlogged condition. The light saturation point (L_s) of sensitive Q10

was 1288μmol m^{-2} s^{-1} under CK and 736μmol m^{-2} s^{-1} under waterlogged condition (Table 3). Significant differences were also found in P_{max} ($p<0.05$) and L_c ($p<0.05$). AQY was also significantly ($p<0.05$) affected by waterlogging stress. Under waterlogged condition, AQY was lower than in CK condition for both genotypes. The reduction in AQY of the tolerant and sensitive genotypes under waterlogged treatments was -22.56% and -30.48%, respectively, compared with CK.

Chl fluorescence: In the tolerant genotype, there were no significant differences ($p>0.05$) between CK and 6 days of waterlogging (Fig. 2). However, in the sensitive genotype, Fv/Fm tended to be less in the waterlogged plants than in the controls after 6 days of waterlogging. Significant decreases ($p<0.05$) in Φ_{PSII} of waterlogged plants were observed in both genotypes (Fig. 3) after 6 days of waterlogging.

Peroxidases, polyphenol oxidases activities and MDA content: In the tolerant genotype, significantly less peroxidase (POD) activity was observed in the waterlogged plants compared with controls after 4 days of waterlogging. In the sensitive genotype, peroxidase activity tended to be higher in the waterlogged plants than in controls after 4 days of waterlogging (Fig. 4).

In the tolerant genotype, there was significantly less activity of PPOs in the waterlogged plants compared with controls after 4days. In the waterlogged plants, sensitive genotype had higher PPOs compared with control plants after 4days (Fig. 5).

In the tolerant genotype, there was significantly higher MDA content in the waterlogged plants compared with controls after 6 days of waterlogging. In the sensitive genotype, MDA content tended to be higher in the waterlogged plants than in the controls after 2 days of waterlogging (Fig. 6).

Table 1. Chlorophyll (Chl) *a*, Chl *b*, Chl a+b of waterlogging-tolerant (Q5) and waterlogging-sensitive (Q10) popcorn inbred lines after 0, 2, 4, and 6 d of waterlogging. Data represent means ± SD of 3 replicates. For each variable, means with different lowercase letters were significantly different ($p<0.05$).

Genotype	Day	Treatment	Chl a[mg g^{-1}]	Chl b[mg g^{-1}]	Chl a+b[mg g^{-1}]
Q5	0	CK	2.81 ± 0.11a	0.76 ± 0.03a	3.57 ± 0.13a
		W	2.89 ± 0.11a	0.78 ± 0.03a	3.67 ± 0.12a
	2	CK	2.73 ± 0.10a	0.72 ± 0.04a	3.45 ± 0.10a
		W	2.70 ± 0.12a	0.70 ± 0.05a	3.40 ± 0.12a
	4	CK	2.45 ± 0.20a	0.66 ± 0.06a	3.11 ± 0.21a
		W	1.94 ± 0.12b	0.69 ± 0.03a	2.63 ± 0.12b
	6	CK	2.26 ± 0.11a	0.58 ± 0.03a	2.84 ± 0.11a
		W	1.85 ± 0.10b	0.59 ± 0.03a	2.44 ± 0.11b
Q10	0	CK	2.57 ± 0.30a	0.74 ± 0.04a	3.31 ± 0.32a
		W	2.51 ± 0.20a	0.72 ± 0.05a	3.23 ± 0.21a
	2	CK	2.47 ± 0.20a	0.68 ± 0.06a	3.15 ± 0.21a
		W	2.49 ± 0.20a	0.69 ± 0.03a	3.18 ± 0.21a
	4	CK	2.08 ± 0.30a	0.55 ± 0.03a	2.63 ± 0.30a
		W	1.54 ± 0.10b	0.48 ± 0.05a	2.02 ± 0.12b
	6	CK	1.77 ± 0.30a	0.50 ± 0.01a	2.27 ± 0.31a
		W	1.21 ± 0.10b	0.45 ± 0.02a	1.66 ± 0.11b

Table 2. Leaf net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), water use efficiency (WUE) of waterlogging-tolerant (Q5) and waterlogging-sensitive (Q10) popcorn inbred lines after 0, 2, 4, 6 d of waterlogging. Data represent means ± SD of 3 representative experiments. For each variable, means with different lowercase letters were significantly different ($p<0.05$).

Genotype	Day	Treatment	P_N [μmol m^{-2} s^{-1}]	g_s [mol m^{-2} s^{-1}]	E [mmol m^{-2} s^{-1}]	WUE
Q5	0	CK	31.43 ± 0.75a	0.19 ± 0.003a	2.96 ± 0.06a	10.62 ± 0.06a
		W	32.13 ± 0.76a	0.19 ± 0.004a	2.86 ± 0.07a	11.23 ± 0.05a
	2	CK	30.28 ± 0.77a	0.18 ± 0.005a	2.84 ± 0.08a	10.66 ± 0.06a
		W	29.89 ± 0.78a	0.17 ± 0.006a	2.76 ± 0.09a	10.83 ± 0.06a
	4	CK	28.43 ± 0.75a	0.17 ± 0.003a	2.56 ± 0.06a	11.11 ± 0.07a
		W	19.95 ± 0.50b	0.13 ± 0.015b	2.10 ± 0.10b	9.50 ± 0.05b
	6	CK	28.85 ± 0.75a	0.17 ± 0.003a	2.66 ± 0.06a	10.85 ± 0.06a
		W	15.45 ± 0.75b	0.12 ± 0.003b	1.66 ± 0.06b	9.31 ± 0.05b
Q10	0	CK	30.28 ± 0.75a	0.17 ± 0.003a	2.64 ± 0.06a	11.47 ± 0.07a
		W	29.43 ± 0.76a	0.17 ± 0.004a	2.55 ± 0.07a	11.54 ± 0.06a
	2	CK	28.59 ± 0.77a	0.18 ± 0.005a	2.64 ± 0.08a	10.83 ± 0.07a
		W	24.48 ± 0.78b	0.14 ± 0.006b	2.28 ± 0.09b	10.74 ± 0.07a
	4	CK	24.03 ± 1.50a	0.18 ± 0.010a	2.36 ± 0.14a	10.18 ± 0.06a
		W	14.37 ± 0.80b	0.09 ± 0.005b	1.61 ± 0.06b	8.93 ± 0.05b
	6	CK	25.03 ± 1.50a	0.18 ± 0.010a	2.56 ± 0.14a	9.78 ± 0.06a
		W	10.27 ± 0.80b	0.07 ± 0.005b	1.41 ± 0.06b	7.28 ± 0.05b

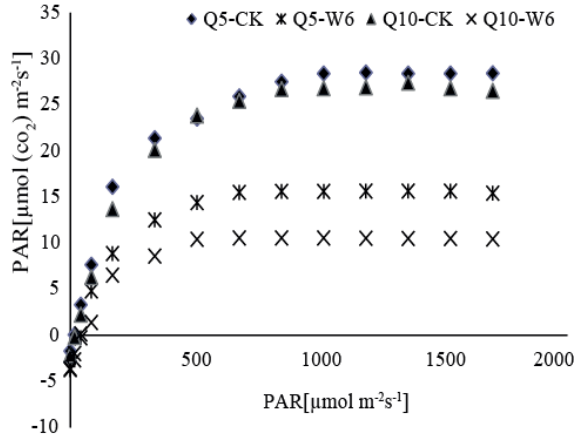

Fig. 1. Response curve of leaf net photosynthetic rate (P_N) as a function of photosynthetically active radiation (PAR) in waterlogging-tolerant (Q5) and waterlogging-sensitive (Q10) popcorn inbred lines after 6 days of waterlogging (CK – control and W6 – 6 days waterlogging).

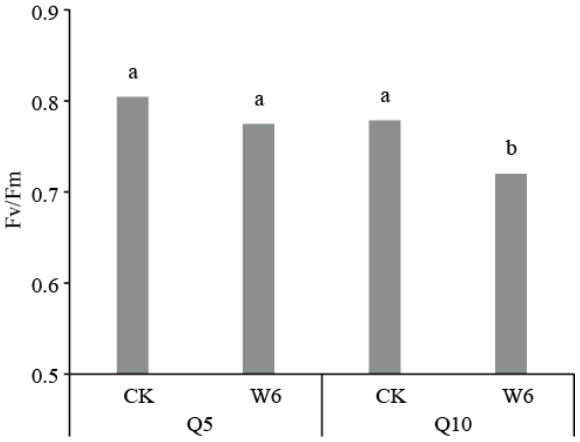

Fig. 2. The maximal quantum yield of PSII photochemistry (Fv/Fm) of tolerant (Q5) and sensitive (Q10) popcorn inbred lines after 6 days of waterlogging (CK – control and W6 – 6 days waterlogging).

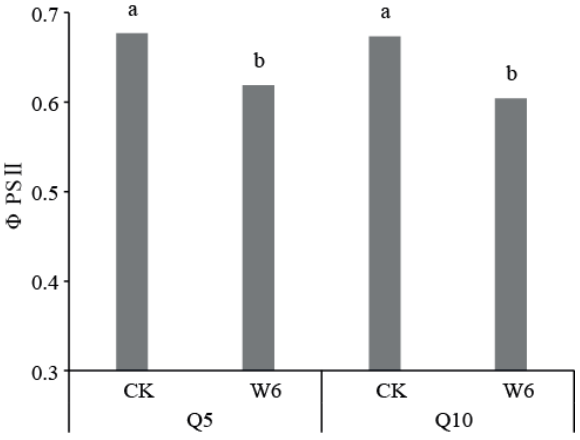

Fig. 3. Effective quantum yield of PSII photochemistry (Φ_{PSII}) of tolerant (Q5) and sensitive (Q10) popcorn inbred lines after 6 days of waterlogging (CK–control and W6–6 days waterlogging).

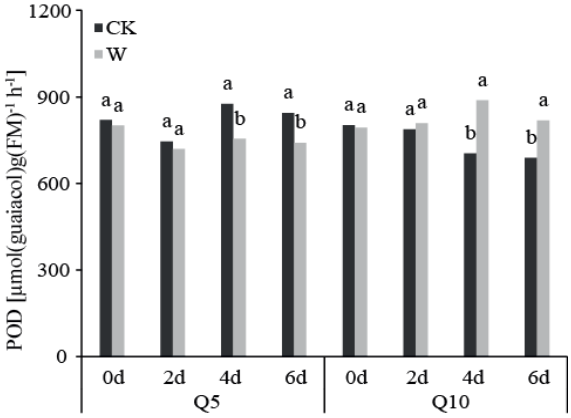

Fig. 4. Peroxidase (POD) activity in leaves of tolerant (Q5) and sensitive (Q10) popcorn inbred lines after 0, 2, 4, and 6 d of waterlogging. Data represent means ± SD of 3 experiments. For each variable, means with different lowercase letters were significantly different at $p<0.05$.

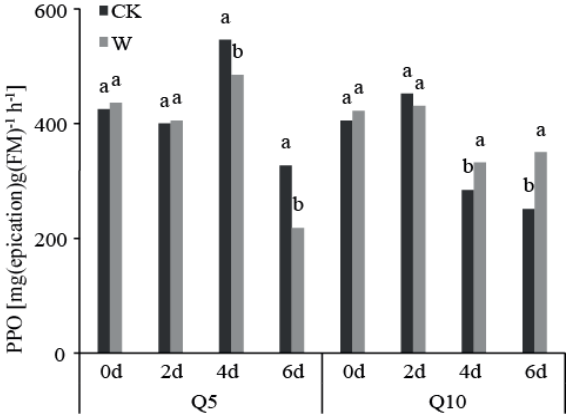

Fig. 5. PPO activity in the leaves of tolerant (Q5) and sensitive (Q10) popcorn inbred lines after 0, 2, 4, and 6 d of waterlogging. Data represent means ± SD of 3 experiments. For each variable, means with different lowercase letters were significantly different ($p<0.05$).

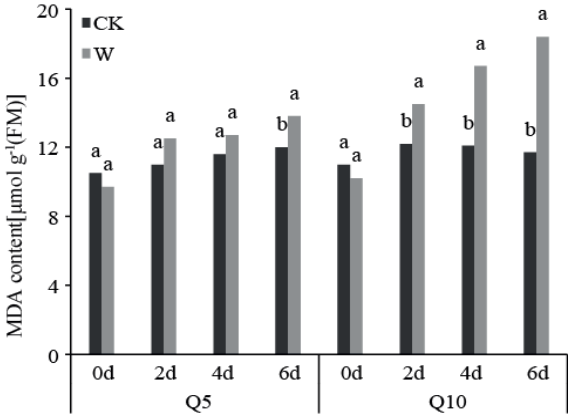

Fig. 6. MDA content of tolerant (Q5) and sensitive (Q10) popcorn inbred lines after 0, 2, 4, and 6 d of waterlogging. Data represent means ± SD of 3 replicates. For each variable, means with different lowercase letters were significantly different at $p<0.05$.

Table 3. Apparent quantum yield (AQY), light compensation point (L_c), light saturation point (L_s), maximal photosynthetic rate (P_{max}) of waterlogging-tolerant (Q5) and waterlogging-sensitive (Q10) popcorn inbred lines after 6 d of waterlogging. Data represent means ± SD of 3 replicates. For each variable, means with different lowercase letters were significantly different ($p<0.05$).

Parameters	Q5		Q10	
	CK	W6	CK	W6
AQY	0.133 ± 0.001a	0.103 ± 0.001b	0.105 ± 0.001a	0.073 ± 0.001b
L_c [μmol m^{-2} s^{-1}]	12 ± 0.90b	36 ± 1.20a	20 ± 0.82b	52 ± 2.02a
L_s [μmol m^{-2} s^{-1}]	1584 ± 55a	996 ± 45b	1288 ± 45a	736 ± 38b
P_{max}	31.43 ± 0.98a	19.88 ± 0.80b	29.69 ± 0.92a	14.33 ± 0.30b

Discussion

Waterlogging is one of the major abiotic stresses limiting the productivity of maize, especially popcorn. Our study sought to identify genetic variation in waterlogging-tolerant and waterlogging-sensitive popcorn inbred lines by assessing the net photosynthesis and other gas-exchange parameters such as E and WUE of popcorn inbred lines under CK compared with waterlogged conditions.

The Chl content was altered in plant leaves under waterlogging, often manifesting chlorosis (Casanova & Brock, 2000). In this experiment, Chla and Chl a+b contents of popcorn leaves decreased under waterlogging conditions in both genotypes, in parallel with the response of P_N (Table 1). These results are consistent with previous studies, which reported that waterlogging usually reduced the leaf Chl levels (Li *et al.*, 2010). In the present study, as expected, waterlogging significantly decreased P_N of popcorn inbred lines (Table 2). Similar effect was also found by Yu (2015) in *Populus euphratica*. High PAR might inhibit P_N by controlling stomatal closure similar to g_s. The decline in g_s results in reduced transpiration under waterlogging (Schaffer *et al*., 1992). Low g_s prevented excessive water loss via transpiration and thus reduced water uptake to maintain a positive water balance (Li *et al.*, 2011). However, in our study, decreased P_{max}, which determines the plant photosynthetic capacity, under waterlogging stress in both genotypes was associated with stomatal closure and improved carboxylation efficiency, suggesting that the photosynthetic capacity of waterlogging-tolerant Q5 was potentially higher than waterlogging-sensitive Q10 under waterlogging conditions. The results are consistent with those of Li *et al*. (2010). Waterlogging stress also decreased AQY in our study (Table 3).

Decline in P_N of some species under waterlogging not only depends on stomatal but also on non-stomatal factors, such as electron transport activity of PS II (Pezeshki, 2001). In our present study, waterlogging reduced F_v/F_m, an indicator of damage to the PS II reaction centers. The decrease ineffective quantum yield of PS II photochemistry ($Ø_{PS}$) was also observed throughout the experimental period (Fig. 2, Fig. 3). However, the decrease in the F_v/F_m of tolerant plants was less than that of the sensitive species, which suggested that the resistant popcorn inbred lines avoided photo damage better than the sensitive ones. This adaptation is attributed to changes in the xanthophyll cycle matching reduced photosynthesis (Qiu *et al*., 2003).

Waterlogging induced oxidative stress, leading to higher production of ROS, such as superoxide ($O2^{\cdot-}$) and hydrogen peroxide (H_2O_2) (Yu & Rengel, 1999, Yordanova *et al*., 2004). The oxygen species levels are controlled by antioxidant enzymes such as peroxidases (Foyer *et al*., 1994). Yordanova *et al*. (2004) found a significant increase in peroxidase activity in *Hordeum vulgare* L. leaves after 72 h of flooding, which was also observed in this study in leaves of sensitive genotype (Fig. 4). In contrast, a decrease in POD activity in the waterlogged plants of the tolerant genotypes suggested a probable activation of fermentative pathways, and reduced mitochondrial activity. The result suggested a decrease in electron transport, reduction in peroxide and superoxide formation, and a reduction in production and activation of peroxidases. The activity of oxidative enzymes such as PPOs, as part of the defense mechanisms also has been studied in plants under stress (Siegel, 1993, Sánchez *et al*., 2000). PPOs oxidize a large group of phenols and are enhanced or inhibited in plants by biotic and abiotic stresses (Vaughn & Duke, 1984, Sánchez *et al*., 2000). This study showed increased PPO activity in the waterlogged plants of the sensitive plant when compared with the controls (Fig. 5). MDA content has been used as an index to assess oxidative damage (Hossain *et al*., 2006, Arbona *et al*., 2008). In our study, waterlogged plants showed significant changes in MDA content compared with the controls (Fig. 6). Increased MDA content in leaves suggests increased oxidative stress (Arbona *et al*., 2008). MDA also facilitated Chl degradation (Upham & Jahnke, 1986) and thus reduced photosynthesis.

In conclusion, popcorn genotypes showed changes in several physiological and photosynthetic variables in response to waterlogging. In addition to decreased levels of photosynthetic pigments, gas exchange, and P_N-PAR curves, it also affects the PS II efficiency. However, the sensitive popcorn inbred lines showed stomatal limitations to photosynthesis, since the decrease in g_s values indicated possible CO_2concentrationfor photosynthesis; non-stomatal limitations to photosynthesis, since the decrease in F_v/F_m values indicated possible damage to the PS II light-harvesting complex; and increased leaf chlorosis, due to decreased photosynthetic pigment content. In addition, the differential physiological and photosynthetic response in the two inbred lines might result in higher tolerance of Q5 than Q10 under waterlogging conditions. These results

suggest that Q5 popcorn inbred lines contribute to genetic diversity of important traits such as P_N, and WUE under waterlogging conditions. Further studies are needed to elucidate the role of anaerobic respiration in the tolerance to soil waterlogging.

Conclusion

Waterlogging induced a decrease in net photosynthesis, stomatal conductance, and transpiration of both tolerant and sensitive genotypes. The waterlogging-sensitive plants showed reduced chlorophyll fluorescence and content and increased peroxidase and polyphenol oxidase activity. The response curves representing the relationship between PAR and P_N for waterlogged plants were similar for both genotypes. The differential physiological and photosynthetic response in the two popcorn inbred lines might be responsible for higher tolerance of Q5 than Q10 under waterlogging conditions. Q5 popcorn inbred lines are a source of genetic diversity for important traits such as P_N and WUE under waterlogging conditions.

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