DOI: 10.1007/s11099-016-0203-0 PHOTOSYNTHETICA 54 (4): 636-640, 2016

BRIEF COMMUNICATION

Morphological and photosynthetic response of waxy corn inbred line to waterlogging

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Abstract

This study aimed to investigate the effects of waterlogging on the growth and photosynthetic characteristics of paired near-isogenic lines of waterlogging-tolerant (Zz-R) and waterlogging-sensitive (Zz-S) waxy corn inbred line seedlings. All plants were grown until the fifth leaves were fully expanded. Subsequently the plants in the pots were submerged in water for 4 d. During the waterlogging period, morphological and photosynthetic parameters related to waterlogging tolerance were examined. After 4 d, a significant decrease was observed in shoot and root fresh mass, net photosynthetic rate, stomatal conductance, transpiration, water-use efficiency, light-saturation point, maximal photosynthetic rate, apparent quantum yield, maximal quantum yield of PSII, and effective quantum yield of PSII photochemistry in waterlogged plants of both genotypes. The Zz-R genotype showed lesser reduction in all mentioned indices when compared to the Zz-S genotype. The inhibition of photosynthesis under waterlogging occurred due to the reduction in stomatal conductance, fluorescence parameters, and chlorophyll content. Thus, our study revealed that the Zz-R genotype can be a source of genetic diversity for important traits such as morphological and photosynthetic parameters.

Additional key words: adventitious root; chlorophyll fluorescence; photosynthesis; pigment; tolerance.

Waterlogging is a serious global problem that affects crop growth and yield, especially in low-lying areas, irrigated areas and areas receiving heavy rainfall. Under waterlogging conditions the soil becomes deficient in oxygen because the gas exchange rate with the atmosphere at the soil surface is reduced (Yu *et al*. 2015). Waterlogging causes a shortfall in oxygen availability to plants, which in turn affects the root system directly and the shoot system indirectly (Capon *et al*. 2009). The formation of adventitious roots is the most common morphological response of plants to root hypoxia (Malik *et al*. 2003, Wei *et al*. 2013).

Plants can adapt to transient waterlogging conditions by developing mechanisms such as adaptation of morphological and photosynthetic characteristics to cope with the stress. Waterlogging usually induced a rapid and significant reduction in the photosynthetic rate of many plant species, particularly waterlogging-sensitive species, such as *Carex cinerascens* (Li *et al*. 2010), *Theobroma cacao* L. (Bertolde *et al*. 2012), and winter wheat (Shao *et al*. 2013). The decline in the photosynthetic rate under waterlogging conditions is associated with the different kinds of responses in plants, including stomatal closure (Dalmolin *et al*. 2013, Fabienne *et al*. 2014, Pereira *et al*. 2014, Yu *et al*. 2015) and decline in chlorophyll (Chl) contents (Li *et al*. 2010, Bertolde *et al*. 2012). Some studies indicated that Chl fluorescence, an efficient tool for detecting changes in functions of photosynthetic parameters, can be used for study of waterlogging (Waldhoff *et al*. 2002, Shao *et al*. 2013).

Maize (*Zea mays* L.) is an important cereal crop. Waxy corn is a kind of maize in which the endosperm contains only amylopectin and no amylase starch molecules (Zhu *et al*. 2014). Commonly, waxy corn seedlings, which are

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Received 9 July 2015, *accepted* 15 January 2016, *published as online-first* 26 January 2016.

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Abbreviations: AQY – apparent quantum yield; Chl – chlorophyll; CK – control; *E* – transpiration; F_v/F_m – maximal quantum yield of PSII; g_s – stomatal conductance; L_s – light-saturation point; L_c – light-compensation point; P_{max} – maximal photosynthetic rate; P_N – net photosynthetic rate; R_D – dark respiration rate; RFM – root fresh mass; SFM – shoot fresh mass; W4 – waterlogging for 4 d; WUE – water-use efficiency; Φ_{PSII} – effective quantum yield of PSII photochemistry.

Acknowledgements: This study was supported by the Cultivation Plan for Youth Agricultural Science and Technology Innovative Talents of Liaoning Province (Grant No. 2014057) and Maize Breeding and Related Technology Research Innovation Team of Liaoning Province (Grant No. 2014201003).

generally grown in low-lying areas, irrigated areas, and areas receiving heavy rainfall, encounter waterlogging, resulting in substrate saturation and partial or complete seedling submergence. Waxy corn seedlings are capable of better tolerance of waterlogging events and can grow better than waterlogging-sensitive waxy corn inbred lines. Hence, the negative effects of waterlogging on waxy corn may be resolved by growing waterlogging-tolerant varieties. Also, no optimal strategies exist for developing cultivars that are better adapted to waterlogging conditions. The challenge is to combine physiological traits in the most effective way so that waterlogging-tolerant or well-adapted germplasm can be produced. Therefore, evaluation under waterlogging conditions appears to be necessary in order to preserve genotypes possessing alleles for waterlogging-tolerance.

This study aimed to evaluate the tolerance and photosynthetic responses of paired near-isogenic lines of waterlogging-tolerant and waterlogging-sensitive waxy corn inbred lines to waterlogging. All plants were grown until the fifth leaves were fully expanded. Subsequently, the plants in pots were submerged in water for 4 d. During the waterlogging period, the morphological and photosynthetic parameters related to waterlogging tolerance were examined. It was expected that waterlogging stress would reduce photosynthesis and the growth of waxy corn inbred line seedlings. It was also expected that waxy corn seedlings of waterlogging-tolerant and waterlogging-sensitive plants would exhibit different morphological and/or photosynthetic adjustments in response to waterlogging.

The experiment was conducted at the Research and Education Center of Agronomy, Shenyang Agricultural University, China, in 2014. Two waxy corn inbred lines were used in this study; these where waterlogging-tolerant genotype (Zz-R) and waterlogging-sensitive genotype (Zz-S). The waxy corn seeds were planted in pots that where 30 cm in height and 25 cm in diameter, respectively. 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 waxy corn was planted. The waxy corn seedlings emerged on 15 May, 2014, and the fifth leaves fully expanded on 8 June. Then two treatments were designed: (*1*) control (CK), in which pots were irrigated every 2 d; each time water was added and allowed to leak from the pot bottom, and (*2*) waterlogging for 4 d (W4), in which all plants were grown until the fifth leaves were fully expanded. Subsequently, the plants in the pots were submerged in water for 4 d, where the water level was maintained at about 10 cm above the soil surface. Each treatment per genotype consisted of 30 pots (three plants per pot). The fifth fully expanded leaves from the bottom of the plant were harvested to carry out all the morphological and photosynthetic measurements at 4 d after waterlogging was initiated.

The adventitious roots of all seedlings were measured at the end of the experiment. The shoot fresh mass (SFM) and root fresh mass (RFM) of each seedling were measured by destructive harvesting.

Net photosynthetic rate (P_N), stomatal conductance (g_s) and transpiration (E) were measured between 9:00 and 11:00 h on the fifth fully expanded leaves of waxy corn after 4 d of waterlogging using an *Li-6400* portable photosynthesis system (*LI-COR*, NE, USA) equipped with an artificial irradiance source *6400-02B RedBlue*. The light intensities for the measurement were set to actual light intensities, and the CO_2 partial pressure was set to 400 μmol s^{-1}. Photosynthetic light responses were measured at 25°C by an internal red and blue radiation source (*LI6400-02*). Fourteen irradiance levels [0, 20, 50, 100, 200, 400, 600, 800, 1,000; 1,200; 1,400; 1,600; 1,800; 2,000 μmol(photon) m^{-2} s^{-1}] were used. The air flux entering into the cuvette was settled at 400 μmol s^{-1}. Maize leaves were acclimated to each PPFD for 4 min, then the steady-state gas exchange properties were logged, and the PPDF in the cuvette were changed. Light-response curves were plotted using the mean values of P_N measured at each PPFD. The light-response data were fitted to a model of nonrectangular hyperbola (Marshall and Biscoe 1980) to estimate the apparent quantum yield (AQY), light-compensation point (L_c), light-saturation point (L_s) and dark respiration rate (R_D). The dark- and light-adapted Chl fluorescence was measured on the same fully expanded leaves using a pulse amplitude modulated leaf chamber fluorometer (*LI-COR*, NE, USA). Instantaneous water-use efficiency (WUE) was determined as the ratio of P_N to E (Sikder *et al.* 2015).

Waterlogging usually causes a reduction in the leaf Chl concentration (Vu and Yelenosky 1991). 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 of ethanol:acetone (1:1, v/v). The flasks were sealed with a plastic wrap and placed in the dark. Leaf fragments were completely white after overnight extraction; the absorbance of the extracted liquid was recorded at 645 and 663 nm against the miscible liquids by a spectrophotometer (*UV-2550, Shimadzu Corporation*, Japan) (Wang 2006). The calculation of Chl *a*, Chl *b*, and Chl (*a*+*b*) contents [mg g^{-1} (FM)] was done based on the following equations (Arnon 1949):

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

$$\text{Chl}\ b = [(22.9\ A_{645} - 4.68\ A_{663}) \times V]/(1{,}000 \times W) \quad (2)$$

$$\text{Chl}\ (a+b) = \text{Chl}\ a + \text{Chl}\ b \quad (3)$$

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

A one-way analysis of variance (*ANOVA*) with least-significant differences was used to test waterlogging effects on the morphological and photosynthetic performance of waxy corn seedlings. Significant differences between control and waterlogging treatments were determined for all morphological and photosynthetic parameters at $P<0.05$. All statistical tests were performed using *SPSS 13.0* (*SPSS*, IL, USA).

All waxy corn seedlings survived under W4. The development of aerial adventitious roots as a typical response symptom to waterlogging was observed in both the waterlogging-tolerant and waterlogging-sensitive waxy corn seedlings. The aerial adventitious roots of both genotypes remarkably increased by 50% and 53.3% for Zz-R and Zz-S, respectively, as a result of W4 compared with those of CK. The waterlogging-sensitive seedling Zz-S exhibited symptoms of stress, such as significant reductions in the SFM and RFM (Table 1). The SFM and RFM for the tolerant genotype of Zz-R decreased less than those of the waterlogging-sensitive genotype of Zz-S.

Waterlogging-tolerant genotype Zz-R, after W4, was not significantly different from CK (Table 1). However, after W4, Chl *a*, Chl *b,* and Chl (*a*+*b*) were significantly lower in the waterlogged plants compared with those of the CK in the waterlogging-sensitive genotype Zz-S.

After W4, a significant decrease in P_N, g_s, *E,* and WUE of waterlogged plants was observed for both genotypes (Table 2). Waterlogging-sensitive genotype Zz-S grown in waterlogged soil showed P_N about 41.1% lower than those of the CK seedlings, and also exhibited a highly reduced g_s (47.1%), *E* (37.1%), and WUE (6.3%). P_N, g_s, *E*, and WUE for waterlogging-tolerant genotype of Zz-R decreased less than those of the waterlogging-sensitive genotype. This pattern also occurred in the F_v/F_m and the effective quantum yield of PSII photochemistry (Φ_{PSII}).

The PAR response curves for the P_N of waterlogged plants displayed a significant decline of P_N after W4 d for both genotypes. The PAR-response curves for the P_N of waterlogging-tolerant genotype Zz-R decreased less than those of the waterlogging-sensitive genotype Zz-S. After W4, a significant decrease in L_s of waterlogged plants was observed for both genotypes (Table 2). The L_s for waterlogging-tolerant genotype Zz-R decreased less than those of the waterlogging-sensitive genotype Zz-S. A significant difference was also found in the maximal photosynthetic rate (P_{max}). Soil waterlogging increased the R_D by 115.0% and 70.3% for waterlogging-tolerant genotype Zz-R and waterlogging-sensitive genotype Zz-S under waterlogged treatments, respectively, compared with that for CK. A significant difference was also found in L_c. The AQY was also significantly affected by waterlogging stress. AQY was lower under the waterlogging condition than under the CK condition for both genotypes. The reductions of AQY of waterlogging-tolerant genotype Zz-R and waterlogging-sensitive genotype Zz-S under waterlogged treatments were 2.1% and 49.5%, respectively, compared with that of CK.

This study showed that waterlogging could reduce the shoot and root growths of waxy corn inbred lines. During waterlogging periods, when the soil is saturated by water, oxygen deficiency can develop rapidly in the roots, causing root damage (Palta *et al.* 2010, Shao *et al.* 2013). The formation of adventitious roots is also the most common morphological response of plants to root hypoxia (Wei *et al.* 2013). In this study, the aerial adventitious roots of both genotypes significantly increased after 4-d waterlogging compared with those of CK (Table 1). Similar results were also found in studies of other plants by Yin *et al.* (2009) and Wei *et al.* (2013). In this study, waterlogging significantly decreased the P_N of waxy corn inbred lines (Table 2). A similar result was also found by Yu *et al.* (2015) in *Populus euphratica*.

High PAR might inhibit P_N by controlling the stomata closure because a similar pattern was observed for g_s. Theoretically, P_{max}, which determines the plant potential photosynthetic capacity, is proportional to the number of active catalytic sites in chloroplasts that are involved in the reductive assimilation of CO_2. In this study, decreased P_{max} under waterlogging stress for both genotypes was associated with stomatal closure, suggesting that the potential photosynthetic capacity of waterlogging-tolerant genotype Zz-R was higher than that of the waterlogging-sensitive

Table 1. Aerial adventitious roots, shoot fresh mass, root fresh mass, and chlorophyll (Chl) *a*, Chl *b*, and Chl (*a*+*b*) content of waxy corn seedlings under CK and waterlogging conditions for 4 d. Data represent means ± SD of three replicates. For each variable, means with *different lowercase letters* are significantly different at $P<0.05$.

Parameter	Inbred line	Zz-R	Zz-S
Aerial adventitious roots [per plant]	CK	4.67 ± 0.58^b	5.00 ± 0.58^b
	W4	7.00 ± 0.58^a	7.67 ± 0.58^a
Shoot fresh mass [g]	CK	10.57 ± 0.06^a	8.60 ± 0.10^a
	W4	10.47 ± 0.06^a	7.60 ± 0.44^b
Root fresh mass [g]	CK	3.67 ± 0.06^a	3.10 ± 0.17^a
	W4	3.43 ± 0.12^b	2.47 ± 0.06^b
Chl *a* [mg g^{-1}]	CK	2.83 ± 0.17^a	2.47 ± 0.39^a
	W4	1.94 ± 0.01^a	1.54 ± 0.13^b
Chl *b* [mg g^{-1}]	CK	0.76 ± 0.03^a	1.02 ± 0.14^a
	W4	0.69 ± 0.23^a	0.57 ± 0.05^b
Chl (*a*+*b*) [mg g^{-1}]	CK	3.59 ± 0.19^a	3.49 ± 0.53^a
	W4	3.33 ± 0.22^a	2.11 ± 0.18^b

Table 2. Leaf net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), water-use efficiency (WUE), maximal quantum yield of PSII photochemistry (F_v/F_m), and effective quantum yield of PSII photochemistry (Φ_{PSII}), dark respiration rate (R_D), apparent quantum yield (AQY), light compensation point (L_c), light saturation point (L_s), and maximal photosynthetic rate (P_{max}) of waxy corn seedlings under CK and waterlogging conditions for 4 d. Data represent means ± SD of three replicates. For each variable, means with *different lowercase letters* are significantly different at $P<0.05$.

Parameter	Zz-R		Zz-S	
	CK	W4	CK	W4
P_N [µmol m^{-2} s^{-1}]	28.53 ± 0.75^{a}	19.90 ± 0.50^{b}	24.23 ± 1.50^{a}	14.27 ± 0.80^{b}
g_s [mol m^{-2} s^{-1}]	0.18 ± 0.003^{a}	0.14 ± 0.015^{b}	0.17 ± 0.010^{a}	0.09 ± 0.005^{b}
E [mmol m^{-2} s^{-1}]	2.86 ± 0.06^{a}	2.10 ± 0.10^{b}	2.56 ± 0.14^{a}	1.61 ± 0.06^{b}
WUE	9.98 ± 0.05^{a}	9.48 ± 0.21^{b}	9.46 ± 0.07^{a}	8.86 ± 0.17^{b}
F_v/F_m	0.80 ± 0.002^{a}	0.77 ± 0.003^{a}	0.77 ± 0.001^{a}	0.73 ± 0.005^{b}
Φ_{PSII}	0.67 ± 0.004^{a}	0.61 ± 0.005^{b}	0.68 ± 0.002^{a}	0.61 ± 0.004^{b}
R_D [µmol m^{-2} s^{-1}]	1.73 ± 0.05^{b}	3.72 ± 0.12^{a}	2.12 ± 0.07^{b}	3.61 ± 0.13^{a}
AQY	0.097 ± 0.001^{a}	0.095 ± 0.001^{a}	0.093 ± 0.001^{a}	0.047 ± 0.000^{b}
L_c [µmol m^{-2} s^{-1}]	16 ± 0.80^{b}	40 ± 1.20^{a}	24 ± 0.85^{b}	80 ± 2.42^{a}
L_s [µmol m^{-2} s^{-1}]	$1{,}416 \pm 52^{a}$	936 ± 41^{b}	$1{,}196 \pm 45^{a}$	644 ± 34^{b}
P_{max} [µmol m^{-2} s^{-1}]	37.2 ± 0.95^{a}	24.2 ± 0.84^{b}	30.5 ± 0.94^{a}	10.2 ± 0.34^{b}

genotype Zz-S under waterlogging conditions (Table 2). In agreement with the study of Li *et al.* (2010), waterlogging stress decreased the AQY in this study (Table 2). The decline in g_s resulted in the reduction of E under waterlogging conditions (Schaffer *et al.* 1992). Low g_s prevented excessive water loss by E; waterlogging affected root metabolism, and thus reduced the water uptake capability to maintain a positive water balance (Kozlowski 1997, Li *et al.* 2011).

Decline in the P_N of some species subjected to waterlogging is not only dependent on stomatal factors but also on nonstomatal factors, such as the electron transport activity of PSII (Pezeshki 2001). In this study, waterlogging resulted in the reduction of F_v/F_m, an indicator of damage to the reaction centers of PSII. The decrease of Φ_{PSII} was also observed throughout the experimental period (Table 2); however, the decrease of the F_v/F_m of waterlogging-tolerant genotype Zz-S was lesser than that of the waterlogging-sensitive genotype Zz-S, suggesting that during waterlogging stress, waterlogging-tolerant waxy corn inbred lines can avoid photodamage better than waterlogging-sensitive ones. This adaptation happens perhaps due to changes in the xanthophyll cycle corresponding to reductions in photosynthesis, which means xanthophyll cycle played an important role in waterlogging-tolerant genotype Zz-R in protecting photosynthetic apparatus from photoinhibitory damge (Qiu *et al.* 2003).

Some factors restricting the photosynthetic activity may include a decreased Chl content under waterlogging conditions (Macek *et al.* 2006, Casanova and Brock 2000). This study demonstrated that the Chl content of waterlogging-sensitive genotype Zz-S significantly decreased after 4 d waterlogging compared with that of CK (Table 1). Differences in the Chl content in the leaves of waxy corn seedlings between two conditions can be assumed as an adaptation to different waterlogging stresses. The waterlogged genotype showed a lower Chl content, which is in agreement with what has also been described for some plants suffering from waterlogging (Li *et al.* 2010).

Under waterlogging conditions, the reduction in photosynthesis was accompanied by an increased R_D in leaves (Table 2). A similar response was found in *Carex cinerascens* plants suffering from waterlogging (Li *et al.* 2010). The increased R_D in waterlogged condition indicated higher energy expenditure to maintain the metabolism in response to waterlogging.

In conclusion, waxy corn genotypes showed changes in several morphological and photosynthetic variables in response to waterlogging. Waterlogging stress not only resulted in the decrease of shoot and root fresh mass, contents of photosynthetic pigments and gas exchange, but also affected the efficiency of PSII. However, the waterlogged plants of the waterlogging-sensitive waxy corn inbred lines showed: (*1*) stomatal limitations to photosynthesis, since the decrease in g_s values indicated possible CO_2 concentration for photosynthesis, (*2*) nonstomatal limitations to photosynthesis, since the decrease in F_v/F_m values indicated possible damage to the PSII light-harvesting complex; (*3*) more aerial adventitious roots to adapt to waterlogging conditions; and (*4*) increased leaf chlorosis, since the photosynthesis pigment contents decreased. In addition, these results suggest that Zz-R waxy corn inbred lines can be a source of genetic diversity for important traits such as P_N and WUE under waterlogging conditions. Further studies can elucidate the role of anaerobic respiration and other regulatory processes in the tolerance to soil waterlogging of waxy corn inbred lines.

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