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Research article

Vulnerability of photosynthesis and photosystem I in Jerusalem artichoke (*Helianthus tuberosus* L.) exposed to waterlogging

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ABSTRACT

Jerusalem artichoke (*Helianthus tuberosus* L.) is an important energy crop for utilizing coastal marginal land. This study was to investigate waterlogging tolerance of Jerusalem artichoke through photosynthetic diagnose with emphasis on photosystem II (PSII) and photosystem I (PSI) performance. Potted plants were subjected to severe (liquid level 5 cm above vermiculite surface) and moderate (liquid level 5 cm below vermiculite surface) waterlogging for 9 days. Large decreased photosynthetic rate suggested photosynthesis vulnerability upon waterlogging. After 7 days of severe waterlogging, PSII and PSI photoinhibition arose, indicated by significant decrease in the maximal photochemical efficiency of PSII (Fv/Fm) and PSI ($\triangle MR/MR_0$), and PSI seemed more vulnerable because of greater decrease in $\triangle MR/MR_0$ than Fv/Fm. In line with decreased $\triangle MR/MR_0$ and unchanged Fv/Fm after 9 days of moderate waterlogging, the amount of PSI reaction center protein rather than PSII reaction center protein was lowered, confirming greater PSI vulnerability. According to positive correlation between $\triangle MR/MR_0$ and efficiency that an electron moves beyond primary quinone and negative correlation between $\triangle MR/MR_0$ and PSII excitation pressure, PSI inactivation elevated PSII excitation pressure by depressing electron transport at PSII acceptor side. Thus, PSI vulnerability induced PSII photoinhibition and endangered the stability of whole photosynthetic apparatus under waterlogging. In agreement with photosystems photoinhibition, elevated H_2O_2 concentration and lipid peroxidation in the leaves corroborated waterlogging-induced oxidative stress. In conclusion, Jerusalem artichoke is a waterlogging sensitive species in terms of photosynthesis and PSI vulnerability. Consistently, tuber yield was tremendously reduced by waterlogging, confirming waterlogging sensitivity of Jerusalem artichoke.

1. Introduction

Large areas of farmlands are in danger of soil flooding worldwide because of high rainfall and poor soil drainage, and the frequency and severity of floods are expected to increase due to climate change (Hirabayashi et al., 2013; Voesenek and Sasidharan, 2013). In these areas, crops have to be confronted with waterlogging stress. Root respiration is initially depressed by waterlogging stress due to soil O_2 deficiency, which is disadvantageous to nutrients and water uptake (Striker and Colmer, 2017; Colmer and Greenway, 2011). As a result, waterlogging stress often reduces crop growth and yield and even endangers plant survival.

As a primary physiological process for plant survival and growth, photosynthesis is liable to be inhibited by environmental stresses. Under waterlogging stress, photosynthesis is less affected in tolerant crop species or varieties in contrast to great reduction of photosynthetic rate in sensitive ones, and particularly, native plants in wetland can better adapt to flood condition without constraint on photosynthesis (Pereira et al., 2014; Pimentel et al., 2014; Waring and Maricle, 2012; Striker and Colmer, 2017; Kumar et al., 2013; Zhu et al., 2016). Therefore, photosynthetic analysis seems as an effective way for diagnosing plant tolerance to waterlogging. Similar to drought and salt

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Abbreviations: Ci, intercellular CO_2 concentration; CE, carboxylation efficiency; ETo/ABS, quantum yield for electron transport; ETo/TRo, probability that an electron moves further than primary acceptor of PSII; Fv/Fm, the maximal quantum yield of PSII; g_s, stomatal conductance; MDA, malondialdehyde; Pn, photosynthetic rate; PSI, Photosystem I; PSII, Photosystem II; RC/ABS, primary quinone reducing reaction centers per PSII antenna chlorophyll; REo/ETo, probability with which an electron from the intersystem electron carriers is transferred to reduce end electron acceptors at the PSI acceptor side; Q_A, primary quinone; ROS, reactive oxygen species; W_k, ratio of relative variable fluorescence at 300 μs to that at J step; $\triangle MR/MR_0$, the maximal photochemical capacity of PSI; ΦPSII, actual photochemical efficiency of PSII; 1-qP, excitation pressure of PSII

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stress, decreased CO_2 availability due to stomatal limitation is considered as the initial negative effect of waterlogging on photosynthesis, as plants need to prevent water loss through leaf transpiration by stomatal closure (Herzog et al., 2016; Pimentel et al., 2014; Irfan et al., 2010; Perez-Jimenez et al., 2017). Leaf carbohydrate may rapidly accumulates in sensitive crops during short term waterlogging stress for several days, because depressed root respiration restricts sugars translocation from shoot to root by lowering sugars consumption in roots, and the accumulated leaf photoassimilates will induce feedback inhibition on CO_2 assimilation (Herzog et al., 2016; Sloan et al., 2016). In contrast, leaf chlorophyll loss may appear possibly due to N deficiency after long term waterlogging, and then lead to non-stomatal inhibition on photosynthesis with declined photochemical capacity of photosystem II (PSII) (Herzog et al., 2016; Wu et al., 2013, 2015). Notably, lowered CO_2 fixation during short term waterlogging has the possibility to induce oxidative stress with excessive production of ROS by inhibiting photosynthetic electron transport (Murata et al., 2007), and may result in PSII photoinhibition and chlorophyll loss as well (Bansal and Srivastava, 2015; Zheng et al., 2017; Zhu et al., 2016). At present, oxidative stress with aggravated leaf lipid peroxidation has been widely illustrated in plants under both short and long term waterlogging (Yin et al., 2009, 2010; Pimentel et al., 2014; Perez-Jimenez et al., 2017; Wang et al., 2016; Zhang et al., 2016a), however, photosystems photoinhibition is not adequately documented compared with stomatal limitation on CO_2 assimilation in photosynthetic process. Moreover, all the studies on waterlogging-induced photoinhibition are concentrated on PSII by detecting the maximal photochemical efficiency of PSII (Fv/Fm) (Bansal and Srivastava, 2015; Wu et al., 2015; Smethurst and Shabala, 2003; Xuma and Naidoo, 2007; Waring and Maricle, 2012; Zhu et al., 2016). Nonetheless, Fv/Fm reflecting photochemical capacity of PSII reaction center can hardly suggest the whole performance of PSII (Li et al., 2009; Schansker et al., 2003), and the responses of PSII donor and acceptor sides to waterlogging stress are still unclear.

PSI photoinhibition is more hazardous than PSII photoinhibition because of the difficult recovery process of PSI (Kudoh and Sonoike, 2002; Zhang and Scheller, 2004). PSI photoinhibition is triggered by ROS produced at the acceptor side of PSI through Mehler reaction, and electron flow from PSII is essential for PSI photoinhibition (Sonoike, 2011; Zhang et al., 2011, 2016b). Therefore, rapid PSII photoinhibition protects PSI from photoinhibition by restricting electron flow to PSI under high temperature or high light stress (Yan et al., 2013a, 2013b; Zivcak et al., 2014), whereas PSI photoinhibition usually arises under chilling stress with low light because of limited restriction on electron flow to PSI (Yang et al., 2014; Zhang et al., 2011, 2014). In our recent studies, PSI photoinhibition also appeared under salt stress, and PSII photoinhibition might derive from elevated excitation pressure due to the feedback inhibition on electron transport at PSII acceptor side by PSI photoinihibition (Yan et al., 2015a, 2015b). Thus, PSI is also a crucial photoinhibition site upon lowered CO_2 fixation through photosynthesis, and PSII and PSI interaction plays an important role in protecting PSI or even the whole photosynthetic apparatus. However, it remains unclear whether PSI is vulnerable to waterlogging, and the interaction between PSII and PSI under waterlogging is largely unknown.

Jerusalem artichoke (*Helianthus tuberosus* L.) which originates from North America is an important industrial crop for ethanol production and medical applications because of high fructose and inulin concentrations in the tuber (Long et al., 2016). With certain salt tolerance and strong adaptability to barren soil, Jerusalem artichoke has become a promising crop for utilizing coastal marginal land in China (Long et al., 2009, 2016). In Yellow River Delta, China, there are large areas of coastal saline lands which often encounter waterlogging in summer due to continuous strong precipitation, and thus, it is necessary to evaluate waterlogging tolerance of Jerusalem artichoke before planting in this area. Unfortunately, there is no report about the effects of waterlogging stress on Jerusalem artichoke at present. In this study, we aimed to investigate waterlogging tolerance of Jerusalem artichoke through photosynthetic diagnosis with emphasis on PSI performance and interaction between PSII and PSI. We hypothesized that Jerusalem artichoke might have certain waterlogging tolerance, and PSII photoinhibition could protect from PSI injury under waterlogging to some extent. Our study may provide a deep insight into photosynthetic response mechanism under waterlogging and assist in crop selection in coastal land with seasonal flooding.

2. Materials and methods

2.1. Plant material and treatment

Tubers of Jerusalem artichoke were collected from Laizhou bay, Shandong province, China. The cultivation procedure was reported in our previous study (Yan et al., 2012). The tubers were planted in plastic pots (25 cm high, 20 cm in diameter) filled with vermiculite (one tuber in each pot) and grown in artificial climatic room (Qiushi, China). The vermiculite was kept wet by watering. The photon flux density was approximately 400 $\mu mol\ m^{-2}\ s^{-1}$ (12 h per day from 07:00 to 19:00) in the room, and day/night temperature and humidity were controlled at 25/18 °C and 70%. After one month, they germinated (one seedling in each pot) and were daily watered with Hoagland nutrient solution (pH 5.7). One month later, health and uniform plants were selected for waterlogging treatments. Potted plants were placed in buckets, and the buckets were filled with Hoagland nutrient solution to adjust liquid level for waterlogging treatments. Plants were subjected to severe (liquid level 5 cm above vermiculite surface) and moderate (liquid level 5 cm below vermiculite surface) waterlogging for 9 days. Thereafter, waterlogging treatments were canceled, and the plants were watered normally with Hoagland nutrient solution under drained condition. Three month later, tubers were collected and weighted. The control plants were watered normally with Hoagland nutrient solution and not exposed to waterlogging. During waterlogging treatment, the newly expanded leaves were sampled for measuring physiological and biochemical parameters.

2.2. Measurements of gas exchange and chlorophyll fluorescence parameters

Gas exchange and modulated chlorophyll fluorescence parameters were simultaneously detected by using an open photosynthetic system (LI-6400XTR, Li-Cor, Lincoln, NE, USA) equipped with a fluorescence leaf chamber (6400-40 LCF, Li-Cor).

Temperature, CO_2 concentration and actinic light intensity were, respectively, set at 25 °C, 400 $\mu mol\ mol^{-1}$ and 1000 $\mu mol\ m^{-2}\ s^{-1}$ in the leaf cuvette. Photosynthetic rate (Pn), stomatal conductance (g_s) and intercellular CO_2 concentration (Ci) were simultaneously recorded. Steady-state fluorescence yield was also recorded, and then a saturating actinic light pulse of 8000 $\mu mol\ m^{-2}\ s^{-1}$ for 0.7 s was used to produce maximum fluorescence yield by temporarily inhibiting PSII photochemistry for measuring actual photochemical efficiency of PSII (ΦPSII). Photochemical quenching coefficient was also noted for calculating PSII excitation pressure (1-qP).

For the measurement of carboxylation efficiency (CE), photon flux density and temperature were set at 1000 $\mu mol\ m^{-2}\ s^{-1}$ and 25 °C in leaf cuvette. Pn was measured under CO_2 concentrations in a sequence of 700, 500, 400, 300, 200, 150, 100, and 50 $\mu mol\ mol^{-1}$. The leaves were kept under each level of CO_2 concentration for 4 min to let leaves reach steady-state photosynthesis, and Pn and Ci were then recorded. The correlation curve of Pn related to Ci was established, and CE was calculated from the linear portion of Pn-Ci curve.