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Grafting Onto *Artemisia annua* Improves Drought Tolerance in Chrysanthemum by Enhancing Photosynthetic Capacity

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A B S T R A C T

Drought stress drastically influences the yield and quality of chrysanthemums, and thus grafting has been widely used to improve tolerance to biotic and abiotic stresses. To explore the mechanisms underlying improvements in drought resistance afforded by grafting, we investigated the changes in growth, gas exchange, ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco) expression and activity, sugar components, and the relative expression of photosynthesis-related genes of chrysanthemum (*Chrysanthemum morifolium* Ramat. 'Hangbai ju') plants grafted onto *Artemisia annua* rootstocks under drought stress by withholding water for 6 d. The results revealed that the growth declines in the grafted chrysanthemums were relatively lower than those of the non-grafted plants under drought stress, and net photosynthetic rate, stomatal conductance, water use efficiency, and transpiration rate in the non-grafted chrysanthemums were significantly decreased. Moreover, the intercellular CO₂ concentrations were significantly increased compared with the grafted plants at 5 and 6 d following drought stress. The grafted plants exhibited higher relative expression of the *CmrbcL*, *CmrbcS*, *CmpsA*, and *Cmcab* genes, as well as higher Rubisco activity and chlorophyll content under the drought treatment. Sugar accumulation also increased under drought stress, particularly in the non-grafted plants. This result suggested that non-grafted chrysanthemums were less able to resist dehydration, and repressed the genes encoding the expression of photosynthetic components. In conclusion, using *A. annua* rootstock could alleviate drought stress in chrysanthemums by improving gas exchange capacity and maintaining *CmrbcL*, *CmrbcS*, *Cmcab*, and *CmpsA* gene expression, thereby increasing Rubisco activity and improving photosynthetic performance.

Keywords: *artemisia annua*; chrysanthemum; grafting; drought stress; sugar components; photosynthetic capacity

1. Introduction

Drought is considered to be one of major abiotic stresses that reduce plant growth and yield (Cruz de Carvalho, 2008). The inhibition of growth under drought stress is related to decreased photosynthetic capacity as a result of declines in chlorophyll content (Bijanazadeh and Emam, 2010) and lower internal CO₂ due to stomatal closure (Bousba et al., 2009), as well as nonstomatal factors such as photosynthetic enzyme activity (e.g., Rubisco) (Ashraf and Harris, 2013). Previous studies have shown that drought stress adversely influences the functionality of both Pho-

tosystem I (PS I) and Photosystem II (PS II), particularly the latter. This results in further subdued electron transport through these two systems (Zlatev, 2009). The quantity of PS II proteins, including LHCII, D1, D2, and mRNA, which accordingly correspond to the *CmpsA*, *CmpsB*, and *Cmcab* genes, is also significantly reduced under drought stress. This was attributed to the depressed rate of transcription and translation, in addition to a faster deterioration of proteins and mRNAs (Liu et al., 2009).

To eliminate these deleterious factors under drought conditions, plants have evolved various protective mechanisms: (1) water conservation by rapid stomatal closure; (2) maintenance

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of higher photosynthetic and metabolic activity by controlling the expression of Rubisco enzymes and associated genes at the transcription level; and (3) acquisition of water mediated by osmotically-active metabolites (such as soluble sugars) (Thapa et al., 2011; Lipiec et al., 2013).

Chrysanthemum (*Chrysanthemum morifolium*) has a long cultural history in China where it has been used in tea and medicine, and has multiple functions including in the prevention of tumorigenesis and lowering of blood stress. It is generally categorized as a drought-sensitive species (Liu et al., 2012b). In recent years, the use of drought-tolerant rootstock in grafting has been acknowledged as an efficient strategy for improving drought tolerance in many types of plants, such as tomato (Albacete et al., 2015), peach (Dirlewanger et al., 2004), cucumber (Li et al., 2016), and poplar (Han et al., 2013). It was suggested that improved drought tolerance in grafted plants was related to the higher supply and transport of water, leaf area, photosynthetic pigment content, and gas exchange capacity (Solari and DeJong, 2006; Koundouras et al., 2008). Previous research has suggested that the herbaceous genus *Artemisia* provides a useful rootstock for enhancing abiotic stress tolerance in chrysanthemum (Deng et al., 2012; Zhang et al., 2013). However, little is known regarding the physiological response and gene expression levels associated with the photosynthetic systems in chrysanthemum plants grafted onto rootstock under drought conditions.

In this study, an excellent tea chrysanthemum cultivar 'Hangbai ju', was grafted onto the rootstock of *A. annua* to gain insight into the mechanisms by which the grafting improved growth. We also examined whether the higher drought tolerance in these plants was associated with increased photosynthetic capacity under drought.

2. Materials and methods

2.1. Plants and treatments

'Hangbai ju' and *A. annua* were obtained from the Chrysanthemum Germplasm Resource Preservation Center at Shandong Agricultural University, China. The field experiment was carried out in a greenhouse from March to July 2016. The soil organic matter was 14.12 g·kg⁻¹, the alkali-hydrolyzed nitrogen was 147 mg·kg⁻¹, the available potassium was 28.95 mg·kg⁻¹, and the available phosphorus was 93.46 mg·kg⁻¹. The chrysanthemum was grafted onto *A. annua* (hereafter referred to as the grafted plants). Seedling cuttings of chrysanthemums plants were used as the control (hereafter referred to as the non-grafted plants).

The seeds of *A. annua* were sowed on March 15th in plastic pots (19 cm in diameter × 17 cm in depth) filled with a 2:1:1 (v/v/v) mixture of garden soil, peat, and vermiculite, and cuttage was conducted in a cutting bed on 6th April. On 3rd May, healthy *A. annua* plants with 30 cm height and 5 mm stem diameter were used as rootstocks, and apical shoots with a length of 14–16 cm and a stem diameter of 3 mm from healthy chrysanthemum 'Hangbai ju' were used as scions. Insert grafting as described by Lee (1994) was performed. On the same day, the chrysanthemum cuttings exhibiting uniform growth were transferred into pots (19 cm in diameter × 17 cm in depth).

On 25th July, morphologically uniform grafted and non-grafted (cuttings) plants were selected for the drought stress treatment. The plants were arranged in a fully randomized manner and the experiment was repeated three times, and each replicate consisted of 16 plants. Drought stress treatment was applied by withholding irrigation for 6 d. During the experiment, the daily minimum/maximum temperature was 19 °C/42 °C, the relative humidity was 30%–60%, and the photosynthetic photon flux density (PPFD) averaged 358 μmol·m⁻²·s⁻¹. Samples were collected on 0, 1, 2, 3, 4, 5, and 6 d, and fully-expanded leaves were frozen in liquid N₂ and then stored at –80 °C for further experimentation. On 0 and 6 d the plants were harvested to measure growth.

2.2. Growth, soil, and plant water status

Soil relative water content (SWC) was measured from 9 a.m. to 10 a.m. in the morning using a handheld soil moisture sensor (Soil Moisture Equipment Corps, Santa Barbara, CA, USA), placed 10 cm below the soil surface in each pot. The leaf relative water content (RWC) was measured every day according to the method described by Sun et al., (2013). Plants were harvested on 0 and 6 d after sufficient watering, and then divided into leaves and roots. The dry mass of the leaves, roots (the part below the graft union), and shoots (the part above the graft union) was determined after drying at 80 °C until constant mass. Specific leaf weight (SLW) was calculated as the dry weight of the leaves per unit leaf of a known area.

2.3. Malondialdehyde content and relative conductivity

Malondialdehyde (MDA) content was measured using the thiobarbituric acid method according to Yin et al., (2009). The MDA content was determined according to its molar coefficient of absorbance of 155 mmol·L⁻¹·cm⁻¹ and expressed as nmol·g⁻¹ FW. The measurement of leaf relative conductivity was conducted essentially as described by Bajji et al., (2002), with a few modifications. The resulting solution conductivity was measured with a conductance meter (FG3-ELK, Mettler-Toledo Co., Zurich, Switzerland).

2.4. Chlorophyll content and photosynthetic parameters

The photosynthetic pigments were extracted in 96% ethanol and the absorbance was recorded with a UV-2450 spectrophotometer (Shimadzu, Kyoto, Japan) at 470, 665, and 649 nm (Bragina et al., 2004). During 9:00 and 11:00, the net photosynthetic rate (P_n), stomatal conductance (G_s), transpiration rate (T_r), and intercellular CO₂ concentration (C_i) of at least five fully-expanded leaves exhibiting uniform growth were measured using a portable infrared gas analyzer (CIRAS-2, PP Systems, UK). Water use efficiency (WUE) was determined by dividing P_n by T_r .

2.5. Rubisco activity determination

Rubisco (EC 4.1.1.39) activity in the leaf samples collected from the central part of a mature leaf was determined according to the method of Sharkey et al., (1991) and Parry et al., (1997). These samples, whose fresh mass was known, were

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