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Photosynthetic gas-exchange and PSII photochemical acclimation to drought in a native and non-native xerophytic species (*Artemisia ordosica* and *Salix psammophila*)

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ABSTRACT

The mechanisms of plant photosynthetic acclimation to drought remains incomplete. We examined the photosynthetic performance through plant photosystem-fluorescence response to a long-lasting, anomalous summer drought (i.e., lasting for 61 days, with soil water content < 0.1 $m^3{\cdot}m^{-3}$) and subsequent post-drought recovery of a native and a non-native desert shrub species (*Artemisia ordosica* and *Salix psammophila*, respectively) growing in northwest China. Key indicators to the examination are derived estimates of plant stomatal conductance (g_s), transpiration (T_r), water use efficiency (WUE), maximum and actual photochemical efficiency (F_v/F_m and Φ_{PSII}), non-photochemical quenching (NPQ), and leaf photosynthesis (P_N) from simultaneous, continuous *in situ* measurements of gas exchange and chlorophyll fluorescence. Chlorophyll fluorescence-associated indicator "F_v/F_m" for both species was down regulated in response to deficits in soil water content (SWC), with differential SWC thresholds of 0.07 and 0.08 $m^3\,m^{-3}$ for *A. ordosica* and *S. psammophila*, respectively. The results revealed that both species acclimate to summer drought by a stomatal-regulation mechanism of reducing g_s and WUE and by a PSII NPQ mechanism of dissipating the excessive light energy, indicative of a water-conservation strategy in the acclimation to drought. In comparison with the non-native species, the native species generally had greater photosynthetic performance under water-deficit conditions demonstrating higher transpiration, net CO_2 assimilation, and greater PSII photochemical efficiency. Lower WUE and greater drought resistance and resilience, combined with minor changes in PSII photochemical efficiency are consistent with a well-defined water-conservation response by *A. ordosica*. The results support the hypothesis that native desert-shrub species can potentially outperform non-native shrub species, due to stronger resistance and faster overall recovery from long-lasting drought. Therefore, with increased drought severity and duration anticipated with future climate change, the native shrub species is suggested to be used in desertification control and ecological restoration for sustainable ecosystem management.

1. Introduction

Arid and semi-arid regions make up ~40% of the earth's land surface and are home to ~20% of the human population (Cao, 2008). The severity and duration of summer droughts in arid and semi-arid areas of the world have been increasing, making severe droughts a significant challenge facing dryland ecosystem management both now and in the near future (Schimel, 2010; Piao et al., 2010; Wang et al., 2014). Photosynthesis is particularly sensitive to environmental constraints (Kalaji et al., 2012). Increasing drought duration may (i) cause photoinhibition in plants, (ii) promote photo-damage of the photosynthetic apparatus, and/or (iii) lead to the reduction of photosynthetic assimilation (Külheim et al., 2002; Schurr et al., 2006; Rodríguez-Calcerrada et al., 2008).

Desert plants have evolved a number of adaptive mechanisms in coping with drought-stressed conditions by adjusting their morphological, physiological, and/or biochemical characteristics (Yordanov et al., 2000; Lei et al., 2006; Marcińska et al., 2013; Amissah et al.,

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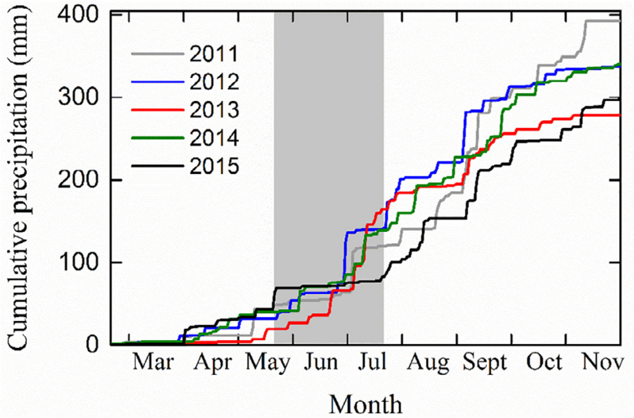

Fig. 1. Annual cumulative precipitation for 2011–2015. The grey band highlights the longest summer period with nominal precipitation among the five years.

2015). Plants in deserts can avoid the effects of droughts by tapping groundwater with deep rooting systems, reducing stomatal opening size and density, promoting waxy surface structures and water-impervious epidermis, and growing small leaves (Brito et al., 2017; Fan et al., 2017). Alongside these morphological changes, desert plants have evolved a variety of physiological and biochemical processes ranging from photosynthetic-related to anti-oxidant defenses (Li and Niyogi, 2001; Allakhverdiev et al., 2008; Doupis et al., 2013). For example, non-photochemical quenching (NPQ) is considered as the fastest process employed by plants to relieve the excitation energy pressure in the photosynthetic membrane (location of PSII reaction) and thus protect plants from stressed conditions (Jahns and Holzwarth, 2012; Ruban et al., 2012; Ware et al., 2015). Under conditions of severe and long-lasting drought stress, photosynthesis-related processes, like CO_2 fixation and stomatal conductance (g_s), are maintained by the photosystem I (PSI) cyclic electron transport, when photosystem II (PSII) processes are inactivated (Haldrup et al., 2001; Georgieva et al., 2005; Feng and Cao, 2005; Chaves et al., 2009; Quaas et al., 2015). Inactivation of PSII, induced by water stress, is often attributed to damage to the photosynthetic apparatus, contributing to reversible photo-damage (Yu et al., 2015; Zhang et al., 2016). However, reports addressing the effects of long-lasting water stress on the functioning of PSII are often in dispute.

Recent *in vivo* studies have shown water stress can lead to the damage of PSII reaction centers (Skotnica et al., 2000; Colom and Vazzana, 2003; Campos et al., 2014), whereas other studies have shown that PSII is mostly resistant to water deficits, showing nominal to no change under extreme water shortage (Massacci et al., 2008; Flexas et al., 2009). Overall, mechanisms leading to PSII damage have yet to be fully explored (Georgieva et al., 2005; Sperdouli and Moustakas, 2012). Although prior studies have provided to our understanding of the relationship between photochemical processes and water-deficit conditions in some areas of the world and for specific biomes, our understanding of photochemical responses in desert shrub species and their physiological acclimation to severe water-deficit conditions remains poor.

Prior studies have examined photosynthetic and photochemical response to drought using manipulative experiments performed at fixed times (Sofo et al., 2009; Balachowski et al., 2016; Ashbacher and Cleland, 2016). Such experiments cannot provide detailed understanding of plant physiological acclimation processes that tend to evolve over time. To permit a holistic understanding of drought influences, we need to examine plant responses during and after a drought event (Flexas et al., 2006; Niinemets, 2010; Grant et al., 2014).

Chlorophyll fluorescence (ChlF) is a non-destructive method currently used in the detection of plant photosynthetic performance (Maxwell and Johnson, 2000; Sperdouli and Moustakas, 2012; Montgomery et al., 2016) and in the investigation of acclimatory and adaptive mechanisms in plants (Bukhov and Carpentier, 2004; Borisovamubarakshina et al., 2015; Rul et al., 2016). Continuous *in situ* monitoring of ChlF provides detailed information on the status and function of photosystem II (PSII; Kalaji et al., 2012), making photosynthetic measurements an important component of plant stress studies. Pulse amplitude modulation (PAM) fluorometry can help with *in situ*, non-destructive monitoring of ChlF of PSII and advance our understanding of acclimation processes in plant species growing in harsh environments (Logan, 2007; Baker, 2008; Durako, 2012; Zha et al., 2017a).

Artemisia ordosica (native shrub species) and *Salix psammophila* (non-native species) are two of the most common shrub species found growing in semi-arid areas of the Mu Us desert land (Wei et al., 2016). *A. ordosica* is a native shrub species distributed mostly on infertile soils (Wu et al., 2015; Lai et al., 2016). *S. psammophila*, in contrast, is a non-native species by large-scale afforestation program in semi-arid area in northwest China to stabilize desert sand dunes, due to its larger size and abundance of horizontally distributed roots (Huang et al., 2001; Xiao et al., 2005; Yang et al., 2008). However, with the prepoderance of irrigation wells and increased human activity throughout area, groundwater is often deeper than 10 m from the surface (Jia et al., 2014), making groundwater largely unavailable to most desert plants. In the region, precipitation is normally the only source of water available for plant use. Furthermore, climate-induced drought events are currently becoming more severe and long lasting than ever before and has been predicted to continually increase in this area (Piao et al., 2010). Consequently, the health of plant ecosystems in semi-arid area are challenged by increasing water limitation. Many studies have found that the sustainability of dominant species is at risk because of water scarcity. Photosynthetic response to drought and post-drought conditions can be species specific (Ruehr et al., 2015) and vary with drought severity and duration (Cai et al., 2015). Related to these expected changes, two important questions arise for stakeholder: (1) can the two dominant species photosynthetic acclimate to water deficit? and (2) if they can, can *S. psammophila* (as the non-native species) survive increasing drought? It is therefore hypothesized that native desert-shrub species can potentially outperform non-native shrub species, showing stronger resistance and faster overall recovery from drought.

The aim of this study was to evaluate the resilience of *A. ordosica* and *S. psammophila* to long-lasting drought conditions with the integration of traditional photosynthetic gas exchange measurements and continuous *in-situ* ChlF monitoring. The study addresses the following scientific questions, namely (1) what are the effects of a major summer drought on leaf photosynthesis; (2) what are the mechanisms that lead to leaf photosynthesis recovery from severe drought; and (3) how do *A. ordosica* and *S. psammophila* differ in their physiological acclimation to summer drought?

2. Method

2.1. Study site and experimental design

The measurements come from plants growing on a sand dune at the Yanchi Research Station of Beijing Forest University (37°42′31″N, 107°13′47″ E, 1530 m above mean sea level), Ningxia, northwest China. The site is located at the southern edge of the Mu Us desert, characterized by sandy soils with a bulk density of 1.6 g·cm^{-3} in the upper 10 cm of the soil profile. The prevailing climate is temperate arid and semi-arid, where rain is scarce, irregularly distributed, and variable from year to year. The mean annual precipitation is 287 mm, 62% of which falls in summer. This area experiences an annual potential evapotranspiration of about 2024 mm. The mean annual temperature is 8.1 °C. All meteorological summaries are based on meteorological data from the Yanchi County meteorological station and represent 51-year averages (1954–2004). On-site vegetation is the result of 10 years of