Plant Physiology and Biochemistry 109 (2016) 397–405

Contents lists available at ScienceDirect

Plant Physiology and Biochemistry

journal homepage: www.elsevier.com/locate/plaphy

Research article

Deciphering the ecophysiological traits involved during water stress acclimation and recovery of the threatened wild carnation, *Dianthus inoxianus*

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A R T I C L E I N F O

Article history:
Received 7 July 2016
Received in revised form
4 October 2016
Accepted 25 October 2016
Available online 27 October 2016

Keywords:
Dianthus inoxianus
Threatened species
Water stress
Photosynthesis
Drought-stress recovery
Climate change

A B S T R A C T

Dianthus inoxianus is an endangered species endemic from a small littoral area in the SW Spain, with an unusual flowering season under the adverse conditions of dry Mediterranean summer. A greenhouse experiment was designed to assess the physiological traits involved in drought acclimation and recovery of 3-month-old plants. The evolution of plant water status, leaf gas exchange, chlorophyll fluorescence, photosynthetic pigments concentrations and a quantitative analysis of photosynthesis limitations were followed during water stress and re-watering. Our results indicated that the plant water status, Ψ_w and RWC, only decreased at the end of the drought period (18th day), together with the net photosynthetic rate, A_N. Photosynthetic impair was mainly caused by diffusional limitations (SL and MCL) of CO_2, as indicated the joint and marked decrease of g_s, g_m and C_i during drought period, while $V_{c,max}$ did not vary. After rewatering, leaf water status recovered faster than photosynthetic one, reaching control values on day 1 after recovery, while A_N, g_m and C_i took 7 days. Additionally, g_s showed the slowest recovery taking 15 days, but g_s decrease was enough to keep Ψ_w and RWC at constant values throughout the experiment. Results suggest a high tolerance and recovery of *D. inoxianus* from severe drought periods. This drought tolerance was also reflected in the stability of its photochemical apparatus and pigments concentrations, as indicated the constant values of F_v/F_m, Φ_{PSII} and pigments concentrations through experimental period. However, prolonged drought events due to global climate change could negatively affect the physiological mechanisms of this species.

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1. Introduction

Mediterranean climate regions are characterized by a regular long dry season which acts as the most important driver of plant community structures (Gasith and Resh, 1999). The increase in the intensity, frequency and duration of extreme drought events as a consequence of global climate change, particularly in the semi-arid Mediterranean climate areas (Schär et al., 2004), may affect composition, structure and biogeography of plant formations (Allen et al., 2010).

Water limitation negatively affects plant productivity, growth and survival by reducing the plant carbon balance (Boyer, 1982; Chaves et al., 2002; Flexas et al., 2006). These negative effects are mediated by water stress-induced stomatal closure which decreases the photosynthetic CO_2 assimilation. This physiological response is regulated by a signal transduction network triggered by the decline in leaf turgor, water potential or low humidity conditions (Chaves et al., 2002), activating the abscisic acid biosynthesis (ABA; Osakabe et al., 2014). Metabolic impairment and leaf internal resistance, decreasing the CO_2 diffusion from stomatal cavity to the sites of carboxylation in the chloroplasts, also contribute to the total limitation of photosynthesis under severe water stress (Flexas et al., 2004). Thus, strategies of tolerance, adaption and survival are of

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Abbreviations: A_N, net photosynthetic rate; BL, biochemical limitations; Chl *a*, chlorophyll *a*; Chl *b*, chlorophyll *b*; C_i, intercellular CO_2 concentration; $Cx + c$, carotenoids; F_v/F_m, maximum quantum efficiency of PSII photochemistry; g_m, mesophyll conductance; g_s, stomatal conductance; iWUE, intrinsic water use efficiency; MCL, mesophyll conductance limitations; md, midday; pd, pre-dawn; RWC, relative water content; SL, stomatal limitations; SWC, soil water content; $V_{c,max}$, maximum carboxylation efficiency of Rubisco; WS, water stressed; WW, well-watered; Ψ_w, leaf water potential; Ψ_π, osmotic potential; Φ_{PSII}, actual photochemical efficiency of PSII.

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http://dx.doi.org/10.1016/j.plaphy.2016.10.023
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major importance for plants growing under adverse environmental conditions (Galle et al., 2009). There are many regulatory mechanisms controlling deleterious changes and adaptive responses to water scarcity (Chaves et al., 2002), as stomatal responses, ion transport, activation of stress signaling pathways (mediated by ABA, proline accumulation or oxidative stress enzymes) and cellular responses to protect the photosynthetic apparatus (Dias et al., 2014; Osakabe et al., 2014; Yi et al., 2016). Photosynthetic recovery limitations are considered key factors in understanding differences between species in resistance and survival to an environmental stress. The underlying processes of photosynthetic recovery from water stress as changes in gene expression (a large fraction of the transcriptome is differentially expressed), metabolite abundance and physiology reveal non-linear relationships that suggest critical thresholds in drought stress responses (Meyer et al., 2014). On the assumed scenario of future climate change, more studies are needed to describe the mechanistic basis for natural variation in drought tolerance and, subsequently, to understand the physiological principles of recovery from drought (Galle et al., 2009).

Dianthus inoxianus Gallego (Caryophyllaceae) is an endangered species endemic to a small littoral area (<100 m.a.s.l.) of the Doñana National Park in the SW Spain (Balao et al., 2007, 2009). *D. inoxianus* is a polyploid species belongs to the recently-radiated Iberian *D. broteri* complex (Balao et al., 2009, 2010). This rare perennial herb has a very small geographic range, inhabiting a narrow ecological niche on dry sandy soils. This wild carnation is threatened by habitat loss, anthropogenic disturbance and intensive herbivory (Herrera and Balao, 2015) which along with the low recruitment due to high seedling mortality during the summer and the highly specialized pollination by a single sphingid species (Balao et al., 2011), put this species in high risk of extinction in the near future. Interestingly, all wild carnations (i.e. genus *Dianthus*) has a marked flowering phenology at summer in contrast to most Mediterranean plants whose flowering period occurs massively in spring, when water conditions, temperature and pollinators activity are more suitable (Mooney et al., 1974; Herrera, 1986; Thompson, 2005). The severe water limitation during the reproductive stage could affect the fitness and floral traits (Carroll et al., 2001; Aragón et al., 2008) as well as the progeny survival (Valladares and Pearcy, 1997). Furthermore, niche-based models suggest a high risk of extinction of *D. inoxianus* because future area is predicted to shift northward, too far from its current position (Felicísimo et al., 2011).

Up-to-date, any study has investigated the ecophysiological effects of the severe water limitation of the threatened *D. inoxianus*. Physiological knowledge mainly focuses on the functioning of plants and, undoubtedly, it is imperative for understanding the habitat requirements of endangered native plants (van Kleunen, 2014; Wikelski and Cooke, 2006). Understanding the physiological response to the increased water-deficit-related stresses as a consequence of global climate change seems crucial for endangered plant species which generally have narrow ecological tolerance and show strong specializations (Schemske et al., 2016; Smith et al., 2005). Therefore, this research improves the understanding of *D. inoxianus* ecophysiological response to drought, which becomes relevant and helpful in a context of global climate change because of its conservation status.

The specific goals of this study were (1) to analyze the effect of extreme water stress and subsequent recovery on the main *D. inoxianus* ecophysiological parameters, including leaves gas exchange, chlorophyll fluorescence, plant-water relations and photosynthetic pigments concentration; and (2) to determine which kind of limitations affect photosynthetic CO_2 assimilation in *D. inoxianus* and evaluate the integrity of their photosystems.

2. Materials and methods

2.1. Plant material and experimental set-up

The experiments were carried out with 3-month-old endemic SW-Iberian carnations (*Dianthus inoxianus* Gallego). Plants were grown in 2.5 L pots containing an organic commercial substrate (Gramoflor GmbH und Co. KG.) and perlite mixture (3:1) inside University of Seville Glasshouse General Services with controlled temperature of 21/25 °C, 40–60% relative humidity and a maximum photosynthetic photon flux density (PPFD) incident on leaves of 1200 $\mu mol\ m^{-2}\ s^{-1}$.

All plants were watered to field capacity at the beginning of the experiment. Then they were divided in two treatments of ten individuals per group and arranged in a randomized plot. One group was kept under well-watered conditions (WW; control) throughout the entire experimental period by adding the amount of water they lost during the day. The other group was subjected to drought (WS; stressed) by withholding water until severe water stress was reached. Therefore, soil water content (SWC) was calculated in both treatments by weighing each pot every day at midday and comparing pots mass with the corresponding mass at field capacity. Severe water stress was considered to have occurred when stomatal conductance to CO_2 (g_s) dropped below 50 mmol $H_2O\ m^{-2}\ s^{-1}$, because photosynthetic activity becomes predominantly inhibited by metabolic processes below this level (Medrano et al., 2002), which happened on the 18th day. When plants reached severe water stress they were re-watered to field capacity and in the following days as the control until g_s and net photosynthetic rate (A_N) were almost restored to well-watered plants values (recovery).

Measurements of leaves water status, gas exchange, chlorophyll fluorescence and photosynthetic pigments concentrations were taken on days 1, 7 and 18 after the onset of the treatments. Additionally, recovery responses were studied for 2 weeks after rewatering.

2.2. Plant water status

Leaf total water potential, Ψ_w, osmotic potential, Ψ_π, and relative water content, RWC, were measured at pre-dawn (Ψ_{wpd}, $\Psi_{\pi pd}$ and RWC_{pd}) and at midday (Ψ_{wmd}, $\Psi_{\pi md}$ and RWC_{md}) on random, fully developed leaves of both treatments ($n = 5$). Ψ_w was measured by a pressure chamber (Model 1515 D - Pressure Chamber Instruments, PMS), while Ψ_π was determined using psychrometric technique with a Vapor Pressure Osmometer (5600 Vapro, Wescor, Logan, USA). RWC was calculated as follow:

$$RWC\ (\%) = [(FW - DW)/(TW - DW)] \times 100$$

where FW was the leaf fresh weight, DW was the leaf dry weight after drying at 60 °C until constant weight was reached, and TW was leaf saturated weight after 24 h rehydration on distilled water at 4 °C in darkness to minimize respiration losses.

2.3. Leaf gas-exchange

Instantaneous gas exchange measurements were taken on random, fully developed leaves ($n = 6$) from each treatment using an open infrared gas-exchange analyser system (Li-6400, Li-COR Inc., Lincoln, NE, USA) equipped with a light leaf chamber (Li-6400-02B, Li-Cor Inc.). Net photosynthetic rate (A_N), stomatal conductance (g_s) and intercellular CO_2 concentration (C_i) were determined at ambient CO_2 concentration of 400 $\mu mol\ mol^{-1}$ air surrounding the leaf (C_a), leaf temperature of 25 ± 2 °C, 50 ± 5%

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