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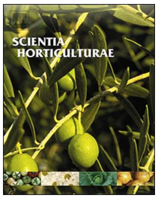

Research Paper

# Drought priming improves subsequent more severe drought in a drought-sensitive cultivar of olive cv. *Chétoui*

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## ABSTRACT

Drought is a major factor limiting crop production worldwide. The objective of this study was to test whether pre-exposure to drought can enhance the subsequent drought response of a drought–sensitive variety of olive cv. *Chétoui*.

Seven-months old olive plants were grown in a controlled conditions and divided into control plants (irrigated daily), primed plants (PP, primed by exposure to drought for 21 days, re-watered for 60 days and then exposed to water depletion for 30 days) and non-primed plants (NPP, well watered for 81 days and immediately followed by intermediate drought as PP). Compared to the non-primed plants, primed plants showed an improvement in biomass production and healthy values of photosynthesis parameters with a higher accumulation of photosynthetic pigments. Additionally, the data of chlorophyll fluorescence were significantly similar to those of control, implying that no photodamage was occurred. Moreover, primed plants exhibited high accumulation of total sugar and proline which lead to the better water status maintenance. The lower level of oxidative status measured in term of hydrogen peroxide ($H_2O_2$), malondiadehyde (MDA) and electrolyte leakage (EC) in primed plants confirmed the alleviation of oxidative stress. Furthermore, the primed plants possessed more effective oxygen scavenging systems as exemplified by the increased activities of CAT, SOD, GP and high accumulation of polyphenols, resulting in a better maintenance in homeostasis of ROS production. Our investigation is indicative of the result of the benefit memory effects caused by stress pre-exposure in young olive plants cv.'*Chétoui*' to overcome subsequent stress.

## 1. Introduction

Olive trees are mainly grown in semiarid regions with Mediterranean climate. Nonetheless, the predicted scenarios of climate change suggest that the Mediterranean basin might be an especially vulnerable region to global warming and drying (Nardini et al., 2014).

Woody plants are constantly exposed to drought, which is one of the most serious problems associated with plant growth and development affecting agricultural demands. Therefore, breeding for drought stress tolerance in trees should be given high research priority in plant biotechnology programs.

Tunisia is the most important olive-growing country of the southern Mediterranean region; over 30% of its cultivated land (1.68 million ha) is dedicated solely to growing olives. The major part of orchard is conducted under rain-fed conditions. Under these conditions, despite the capacity of olive trees to tolerate drought, they usually showed a decrease in photosynthesis resulting in a reduction of the vegetative growth and a significant decline of the productive performance, low yield and alternate bearing behavior (Ben Ahmed et al., 2007). Drought could severely affect also the olive fruit quality (Proietti and Antognozzi, 1996).

This problem will be further aggravated in the variety *Chétoui,* second main variety cultivated in Tunisia, which response to stress have proved to be quite sensitive to drought (Guerfel et al., 2009). In fact, it has been reported that the response of olive to water stress is a cultivar-dependent characteristic and considerable genetic variation for drought tolerance has been observed (Bacelar et al., 2007). Furthermore, *Chétoui* is an extremely important variety due to its healthy oil, highly valued for its richness in phenolic compounds and tocopherols (Ben Temime et al., 2006) which guarantees to this variety a stability against high levels of oxidation; its sensorial characteristics are much appreciated by consumers. Moreover, their leaves are a good source of

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phenols particularly flavonoids which possess potent antioxidant activity. Therefore, efficient strategies for improving drought tolerance of this variety are needed.

Plant priming is a process by which an earlier exposure to abiotic stress may alter a plant's subsequent stress response by producing faster and/or stronger reactions that may provide the benefits of enhanced protection (Walter et al., 2011; Li et al., 2014), referred to as stress memory (Li and Liu, 2016), it has been reported in diverse plant species (Li et al., 2016). Stress memory involves accumulation of signaling proteins or transcription factors and epigenetic mechanisms in plants (DNA methylation or acetylation, chromatin remodeling or histones alteration) that result in gene silencing and/or activation, leading to an improvement in the stress response when plants are exposed to a subsequent stress event (Bruce et al., 2007; Han and Wagner, 2014). The time span between stress events (for example, rehydration following drought) might be an important factor (Bruce et al., 2007). In this time, there appears to be a mechanism for storing information from previous exposure. Retaining this information or the imprint/memory of the stress can be for short or long term duration (Ga'lis et al., 2009; Li et al., 2016). It has been reported that epigenetic mechanism, underpins more longer lasting effect in memory process (Bruce et al., 2007), but stress memory is retained for only short period if the memory depends on the half-life of stress induced proteins, RNAs or metabolites (Bruce et al., 2007). Unfortunately, in plants, experiments to elucidate stress imprints normally undertake time intervals of less than 1 week, which is short in relation to a plant life span (Bruce et al., 2007). Nevertheless, Walter et al. (2011) demonstrated that *Arrhenatherum elatius* plants kept a drought stress imprint over several months, which remained evenafter a harvest.

For instance, drought priming can enhance tolerance to subsequent drought by improved biomass (Walter et al., 2011), leaf photosynthesis (Li et al., 2011a; Walter et al., 2011; Wang et al., 2015) and photoprotection (Walter et al., 2011). It is well known that photosynthesis is one of the most sensitive processes affected by abiotic stress. Water deficit decreases photosynthetic rates via decreased $CO_2$ diffusion, which is caused by both stomatal and non-stomatal mechanisms. The limitation of $CO_2$ assimilation causes the over-reduction of photosynthetic electron chain, which is the major source of reactive oxygen species (ROS) under stress conditions. At high levels, ROS can have detrimental effects on plant metabolism, causing oxidative damage to proteins, nucleic acids and lipids essential to membrane structure (Apel and Hirt, 2004). It has also been shown that drought priming can led to better maintenance of membrane stability, and low level of ROS accumulation (Wang et al., 2014a) through enhancing the antioxidant capacity in primed plants in comparison with non-primed plants. It is also known that the harmful effects of ROS in plants can be reduced or eliminated by endogenous scavenging mechanisms, including both enzyme and non-enzyme defense systems (Møller et al., 2007). The enzymatic defense systems composed by several enzymes are involved in the detoxification of ROS such as superoxide dismutase (SOD), catalase (CAT), guaiacol peroxidase (GP), ascorbate peroxidase (APX) and other enzymes of the ascorbate-glutathione cycle. Although plants containing high concentrations of non enzymatic antioxidants, notably, phenolic compounds possess ideal chemistry for free radical scavenging actively acting as plant antioxidants (Petdridis et al., 2012). Furthermore it has been reported that drought priming confers to primed plants the ability to retain water more efficiently than non primed plants (Wang et al., 2014a). Osmotic adjustment has been considered as an important physiological adaptation character associated with drought tolerance. The capability of synthesizing organic compatible solutes, which act as osmoregulators such asproline and sugars, is a well-known adaptive mechanism in theolive tree against drought conditions (Sofo et al., 2004).

The primarily data on drought priming and memorization process are on herbaceous species but very little information is available on woody species, as no evidence has been reported on the beneficial effect of learning and remembering from the first stress exposure on young olive plants in facing water stress. In this investigation, we tested if olive plants had the capacity for some form of "stress imprint" from the previous water stress exposure and whether we can explore this ability to improve its performance against such environment conditions. Emphasis was on physiological parameters, osmoregulation and oxidative system in young olive plants during previous drought (drought priming), recovery and subsequent drought (intermediate drought). This physiological approach 'drought priming' can be applied to improve drought tolerance with respect of environmental ecosystems for effective and sustainable olive plants protection in a friendly way.

## 2. Materials and methods

### 2.1. Plant material and growth conditions

Seven-months-old self rooted plants (*Olea europaea* L.) cultivar '*Chétoui*', were transplanted in 10 L pots filled with inert sand with fine texture. Plants were grown under glasshouse with day/night temperature regime of 25/17 °C, 16 h photoperiod, light intensity of 400 mmol $m^{-2}$ $s^{-1}$, and 70–75% relative humidity. Plants were grown for 3 weeks and then divided as follow:

C: control plants, irrigated every two days with 100 mL of 100% Hoagland solution during 111 days experiment.

NPP: non-primed plants, well watered for 81 days and then stressed by water depletion for 30 days (denoted as Intermediate drought).

PP: primed plants, primed by exposure to drought for 21 days of water deficit, rewatered for 60 days and then exposed to water depletion for 30 days (intermediate drought) as NPP.

In details; the first step was to divide plants into 2 groups: (1)-Control (C1; 10 plants): plants were irrigated every two days for 21 days. (2)-Drought (D; 10 plants): plants were subjected to water depletion for 21 d. Thereafter, all plants are subjected to a rewatering period during 8 weeks (RW; 10 plants) and this group had a control group in the same age (C2; 10 plants). Afterwards, each plants group was exposed to either of the following drought period: The first group (control): was divided into 2 sub-groups: the first one was kept as a control (C3; 15 pots) and the second (NPP; 15 pots) was subjected to a drought treatment for 30 d (first and single drought exposure). The second group (PP; 15pots): was also resubjected to a water stress for 30

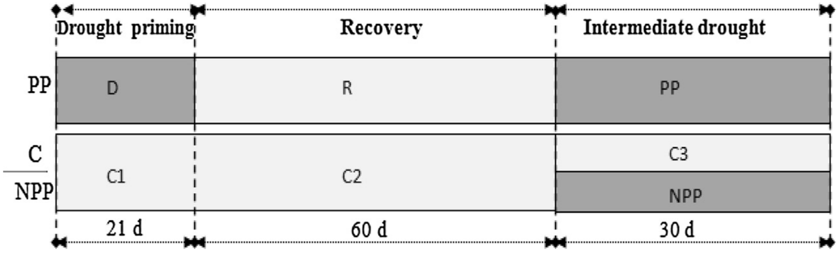

**Fig. 1.** Diagram of the experiment design; **C**: control plants, well watered during 111 d experiment. NPP: non-primed plants, well watered for 81 d and then stressed by withholding water for 30 d (denoted as Intermediate drought). PP: primed plants, primed by exposure to drought for 21 d of water deficit, re-watered for 60 d and then exposed to water depletion for 30 d.