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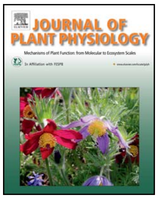

Effects of olive root warming on potassium transport and plant growth

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ABSTRACTS

Young olive (*Olea europaea* L.) plants generated from seed were grown in liquid hydroponic medium exposing the roots system for 33 days or 24 h to high temperature (37 °C) while the aerial part to 25 °C aiming to determine the prolonged and immediate effects of root warming on $K^+(Rb^+)$ transport in the root and consequently on plant growth. The exposition of the root system to 37 °C for 24 h inhibited K^+ (Rb^+) transport from root to shoot having no effect on its uptake. However, when the root system was exposed permanently to 37 °C both the K^+ (Rb^+) uptake and translocation to the aerial part were inhibited as well as the growth in all plants organs. The ability of the root system to recover K^+ (Rb^+) uptake and transport capacity after being exposed to high temperature was also evaluated. Plants grown in a root medium at 37 °C for 31 days were transferred to another at 25 °C for 48 or 96 h. The recovery of K^+ (Rb^+) root transport capacity after high root temperature was slow. Any signal of recovery was observed after 48 h without stress: both potassium root uptake and subsequent transport to above organs were inhibited yet. Whereas 96 h without stress led to restore potassium upward transport capacity although the uptake was partially inhibited yet. The results obtained in this study have shown that the root system of young olive plants is very sensitive to high temperature related to root potassium transport and growth of the plant. Taking into account the two processes involved in root potassium transport, the discharge of K^+ to the xylem vessels was more affected than the uptake at the initial phase of high root temperature stress. However, it was the first process to be re-established during recovery. All this could explain the symptoms frequently observed in olive orchards when dry and high temperature spells occur: a reduction in shoots growth and leaves with low levels of potassium contents and dehydration symptoms.

1. Introduction

The Mediterranean basin is the largest area in the world with a specific climate for olive (*Olea europaea* L.) cultivation; however, if current trends in greenhouse gas emissions continue, the environmental conditions of this region are expected to change in the near future. In particular, air temperature has been projected to rise drastically (Giorgi, 2006; Giorgi and Lionello, 2008; Gualdi et al., 2013). Soil temperature is generally lower than that of the air, although seasonal fluctuations occur depending on aboveground factors. The increase in atmospheric temperature is therefore expected to be accompanied by a gradual rise in soil temperature, especially in the upper soil layers (IPCC, 2014).

Temperature is a primary environmental factor for plant growth and development. Each species has an optimal thermal range, so when temperature lies outside this range, the physiological and biochemical processes involved in plant growth are impaired, resulting in growth decline (Mahan et al., 1995; Wahid et al., 2007). The optimum temperature for olive vegetative development ranges from 10 to 30 °C, provided that nutrient and water availability is not a limiting factor. It has been suggested that temperatures above 35 °C could limit olive vegetative growth (Rallo and Cuevas, 2008; Therios, 2009). Recently, a reduction in plant dry matter accumulation has been observed in olive mist-cuttings and young plants generated from seeds, when the whole plants were exposed to moderately high temperatures (37° C) (Benlloch-Gonzalez et al., 2016). Considering that temperature values in the Mediterranean region are predicted to exceed the optimal levels for olive performance, this crop is likely to experience frequent periods of temperature stress of both long and short duration, which may affect growth, development and productivity.

Most of the studies addressing plant adaptation to warmer temperatures have been focused on plant responses to increasing air temperature (Paulsen, 1994; Wahid et al., 2007) and pay little attention to the underlying processes which occur when the soil warms up. Given

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that the microbial activity, mineralization processes and movement of ions in the soil are temperature-dependent (Zak et al., 1999; Hussain and Maqsood, 2011), higher temperatures may contribute to loss of soil fertility and diminish the availability of nutrients for plants (St Clair and Lynch, 2010). The scarcity of soil water and mineral nutrients under warmer conditions could negatively affect crops, as they are primary soil resources for plant growth. Among the essential mineral nutrients, K^+ is directly involved in plant growth processes: its accumulation in the cell contributes to the creation of the osmotic component of the water potential needed to absorb water (Kramer, 1983) and generates the cell turgor required for cell elongation (Wyn Jones et al., 1979; Mengel and Arneke, 1982; Hsiao and Läuchli, 1986; Shabala and Lew, 2002; Chen et al., 2007). At the whole plant level, K^+ plays a key role in the regulation of water movement through the plant: it is involved in the osmotic absorption of water by the root (Laüchli, 1984) and in the control of transpiration (Hsiao and Läuchli, 1986). So when a plant is supplied adequately with K^+, its tissues are better hydrated (Mengel and Kirkby, 2001), which favors plant growth and resistance to unfavorable environmental conditions, including heat stress (Gur and Shulman, 1971; Gur et al., 1976; Cakmak, 2005; Zörb et al., 2014). From this information, it can be deduced that the root system may play a critical role in the plant's adaptation to warmer conditions by absorbing enough K^+ to keep the cytosolic K^+ at its optimal level.

It seems that high soil temperature has a greater detrimental effect than high air temperature on the decline in plant growth and mineral nutrient accumulation in various species (Ruter and Ingram, 1990; Udomprasert et al., 1995; Huang and Xu, 2000; Xu and Huang, 2000a,b). However, the influence of high soil temperatures on root growth and functioning and the impact on root-shoot relationships has not been researched in depth (BassiriRad, 2000; Huang et al., 2012). This is of great importance in olive orchards, where the irrigation systems commonly used mean that the most active roots are located in the upper soil layers (Fernández and Moreno, 1999) which are the most exposed to high temperatures, because these soils tend to have poor plant cover. Despite growing recognition of this fact, there is little information on how warmer soil temperatures will affect olive root growth and the uptake of K^+ and its subsequent allocation to the different plant organs, which results in plant growth. The accumulation of a high level of K^+ in plant tissues under warmer conditions would support both the growth of developing organs and the transpiring leaf area, contributing in this way towards alleviating the possible detrimental effects of high temperatures.

Plants are able to adjust to variations in the availability of K^+ through changes in root architecture and the activation or inhibition of K^+ transporter systems (Nieves-Cordones et al., 2014). Nevertheless, the potential effects of high temperature on these mechanisms and the consequences on plant K^+ nutrition are not clear. The movement of ions through the cell membranes seems to be very sensitive to changes in soil or root temperature (Chapin, 1974; BassiriRad et al., 1993). As temperatures rise, membrane protein-transporters change their configuration (Epstein and Bloom, 2004). A reduction in the absorption of K^+ (Rb^+) has been observed in whole sunflower plants, isolated corn roots, and tomato plants when the temperature of the root medium was above 33, 30 and 35 °C respectively (Benlloch et al., 1989; Bravo-F and Uribe, 1981; Falah et al., 2010). In a recent study using tomato plants, the reduction in root K^+-uptake rate under high root medium temperature was correlated to a decrease in the concentration/activity of the potassium transporter KT1 (Giri et al., 2017). In creeping bentgrass, exposure of the root system to high soil temperature (35 °C), while maintaining the shoot at normal temperature significantly reduced potassium uptake by the root (Huang and Xu, 2000).

In summary, the olive root system will be exposed to short and long periods of high temperature stress in the future, however, how this organ will cope under these circumstances is unknown. It is not clear how high temperature in the root will affect K^+ transporter systems involved in K^+ nutrition and the possible effects on plant growth. In order to clarify these questions, the aim of the present study using young olive plants generated from seeds is twofold. Firstly, it examines the immediate and prolonged effect of moderately high temperature applied in the root medium on K^+ (Rb^+) uptake and its subsequent allocation to the different plant organs and, consequently, plant growth. Secondly, it evaluates if the K^+ (Rb^+) uptake and transport capacity of the root system is recovered after being exposed to a period of high temperature. Interpreting root responses to temperature is often a complicated task, due to interactions with experimental conditions and surrounding environmental factors. Therefore, in this study, root medium and shoot air temperatures were controlled independently and the nutritional status of the root surface was maintained relatively constant. The plants were grown in a liquid hydroponic system, to ensure that potential changes in root functions were not due to any alterations in the nutrient supply.

2. Material and methods

2.1. Plant material and growth conditions

Olive (*Olea europaea* L.) 'Arbequina' seeds were soaked in a Ziram fungicide solution ($2\,g\,L^{-1}$) for 5 min and stratified on filter paper moistened with water, in covered petri-dishes, at 14 °C for 21 days. After stratification, the seeds were sown in recipients with perlite, moistened with water and placed in a germination chamber at 25 °C. After 10 days, the seedlings were individually transferred into 680-mL flasks containing a Hoagland's type nutrient solution (NS) and placed in a controlled growth chamber with a relative humidity between 60 and 80%, a temperature of 25/22 °C (day/night), a photosynthetic photon flux density of $350\,\mu mol\,m^{-2}\,s^{-1}$ (fluorescent tubes, Sylvania cool-white VHO) and a photoperiod of 14 h of light. The NS had the following composition: 2.5 mM $Ca(NO_3)_2$; 2.5 mM KCl; 0.25 mM $Ca(H_2PO_4)_2$; 1.0 mM $MgSO_4$; 12.5 μM H_3BO_3; 1.0 μM $MnSO_4$; 1.0 μM $ZnSO_4$; 0.25 μM $CuSO_4$; 0.2 μM $(NH_4)_6Mo_7O_{24}$ and 10 μM Fe-ethylenediamine-di-o-hydroxy-phenylacetic acid. The NS was continuously aerated and renewed every week during the whole experiment. The plants were grown under these conditions for acclimation between 14-17 days, depending on the experiment, before the root temperature treatments were started.

2.2. Root temperature treatments

After acclimation, the root system of a group of plants was maintained at the ambient temperature of the growth chamber (25 °C), while in other the temperature of the root medium was increased to 37 °C. To reach this temperature in the root medium, the flasks were placed in a water bath at 37 °C positioned in the growth chamber. An immersion-heater regulated by a thermostat kept the roots at the desired temperature. To maintain a constant temperature of 37 °C in the entire root zone of the plants, the water level was kept at the top edge of the bath throughout the experimental period. In all the plants, the aerial part was exposed to the ambient temperature of the growth chamber (25 °C). The plants were kept under these conditions for 33 days. In order to determine the immediate effect of high temperature in the root system, a set of plants grown in the root medium at 25 °C, 24 h prior to the end of the experiment, was introduced in a water bath at 37 °C. In this way, three root temperature treatments were applied: 25 °C, 37 °C and 25/37 °C (24 h) with the aerial part kept at 25 °C in all cases. To study the recovery capacity of the root system after being exposed to a high temperature period, another experiment was performed. Firstly, the root system of the plants was exposed to either 25 or 37 °C, with the aerial part kept at ambient temperature (25 °C), for 31 days. The same procedure described above was followed. After that, those plants whose root systems were exposed to 37 °C were taken out of the water bath and kept at the ambient temperature, 25 °C, for recovery for either 48 h [37/25 °C (48 h)] or 96 h [37/25 °C (96 h)].