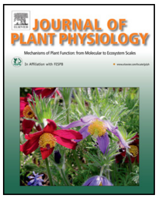
Journal of Plant Physiology 226 (2018) 56–63

Contents lists available at ScienceDirect

Journal of Plant Physiology

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



The role of nighttime water balance on *Olea europaea* plants subjected to contrasting water regimes

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ARTICLE INFO

Keywords:
Olive tree
Stomatal opening
Transpiration
Drought
Nocturnal warming

ABSTRACT

The climate change scenarios besides foreseeing a severe drought imposition also emphasize the temperature rising in the Mediterranean region, with special prominence at nighttime. Despite the high olive tree tolerance to severe environmental conditions, stomatal nighttime water loss can change plant water relations, and the related consequences and opportunities, especially under water scarcity, must be clarified. A set of 3-year-old potted olive trees were subjected to three cycles of drought, imposed by withholding irrigation, while another group were continuously irrigated. At the end of the latter and more severe drought cycle, daytime gas exchange parameters, water status and membrane integrity was negatively affected by drought imposition. Moreover, the nighttime transpiration rate was far above cuticular water loss, suggesting sustained stomatal aperture during nighttime, leading to substantial water losses, which was higher under drought in the first hours of darkness. The higher nighttime stomatal conductance of droughted plants were related with higher starch concentration in their leaves, a thicker trichome layer and a lower intercellular CO_2 concentration, in a closely association with an inferior nighttime respiration. Still, whole-plant transpiration on droughted plants were much lower than leaf transpiration-based estimates, which is interpreted as compensation by water inputs due to dew deposition on leaves. Although unexpected, the increased of stomatal conductance in the first hours of the night, until a certain level of water deficit intensity, could be linked with potential benefits to the plants.

1. Introduction

Drought and high temperature stresses impair several physiological processes, like photosynthesis and water status (Fernández, 2014), and seriously affect membrane stability, increasing the permeability and leakage of ions (Elbasyoni et al., 2017), that may lead to decrease vegetative growth and yield. Moreover, those negative effects can be exacerbated by the projections of climate change in the Mediterranean, which anticipate a general reduction in rainfall and an increase in temperature, the last one more markedly at nighttime (IPCC, 2013). Since nocturnal warming could affect plants in several ways, the nighttime transpiration and respiration are worth considering. However, as far as we know these aspects are been poorly investigated.

Although nighttime stomatal opening is unexpected because there is no opportunity for carbon gain and the need to cool leaves is reduced or absent (Caird et al., 2007), a substantial leaf nighttime stomatal conductance (g_{night}) and transpiration (E_{night}) was observed in a wide range of species from different functional groups and ecosystems (Dawson et al., 2007; Ogle et al., 2012; Resco de Dios et al., 2015; Snyder et al., 2003). However, there are several factors that can determine those responses, such as soil water (Caird et al., 2007; Dawson et al., 2007; Howard and Donovan, 2007; Escalona et al., 2013; Zeppel et al., 2014) and nutrient availability (Caird et al., 2007), vapor pressure deficit (VPD) (Daley and Phillips, 2006; Caird et al., 2007; Dawson et al., 2007; Zeppel et al., 2014), wind speed (Daley and Phillips, 2006; Dawson et al., 2007), CO_2 concentration (Caird et al., 2007; Zeppel et al., 2014), dusts, aerosols and dew and/or fog (Burkhardt, 2010), previous day environmental conditions (Caird et al., 2007; Easlon and Richards, 2009), net photosynthesis (A_N) (Easlon and Richards, 2009) and stomatal conductance during the day (g_{day}) (Snyder et al., 2003), carbohydrate metabolism (Easlon and Richards, 2009; Resco de Dios et al., 2015), circadian rhythms (Caird et al., 2007; Resco de Dios et al., 2015) and leaf age (Caird et al., 2007; Zeppel et al., 2014). The occurrence and magnitude of g_{night} and E_{night} display conflicting patterns and the generalization about the factors that affect those traits is still not possible. Additionally, there are strong evidences that the responses are both species and cultivar dependent (Daley and Phillips, 2006; Escalona et al., 2013; Flexas et al., 2010; Ogle et al., 2012; Snyder et al., 2003).

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https://doi.org/10.1016/j.jplph.2018.04.004
Received 5 January 2018; Received in revised form 13 March 2018; Accepted 8 April 2018

Although recently we have noticed a growing awareness about g_{night} and E_{night}, their implication in physiological processes remain unclear (Coupel-Ledru et al., 2016; Escalona et al., 2013; Ogle et al., 2012). The g_{night} and, consequently, E_{night} affect plant water balance, water use efficiency (WUE) (Escalona et al., 2013) and hydraulic redistribution (Howard et al., 2009). In fact, substantial water losses have been reported to occur overnight at leaf and plant scales, strongly impacting global evapotranspiration (Forster, 2014; Resco de Dios et al., 2015). Nevertheless, it has also been postulated several benefits related with the continue water loss during the night that may outweighs those costs, including the improvement of nutrient uptake (Scholz et al., 2007; Snyder et al., 2008; Snyder et al., 2003), preventing excess cell turgor at night when water availability increases and leaves still contain substantial contents of osmoticants (Donovan et al., 1999, 2001), supplying O_2, enhancing the capacitance of the trunk and stem (Daley and Phillips, 2006) and preventing CO_2 build-up in leaves from nighttime dark respiration (R_{night}) (Marks and Lechowicz, 2007). The prevalence of g_{night} and E_{night} in some conditions and the potential influence in plant growth and physiology can indicate a widespread behavior and an adaptive process that must be clarified. Furthermore, those outcomes have implications in plant water relations theory and in the studies, that utilize plant water use data at larger scales (Dawson et al., 2007).

Olive tree (*Olea europaea* L.) is a common species of Mediterranean region that displays important morphological and physiological adaptive mechanisms to withstand the environmental constraints that characterizes Mediterranean climate. This capacity, includes the ability to control leaf transpiration by a high thickness and density of the leaves, associated to a dense peltate trichomes layer (Bacelar et al., 2004). Additionally, also involves an efficient capacity to regulate stomatal aperture, and the effective ability to extract water from soils with very low water potential and/or to sustain very low internal water deficits (Connor and Fereres, 2005). However, there is a lack of information and understanding about g_{night} and E_{night} mechanisms in *Olea europaea*. Arquero et al. (2006) mentioned a very low stomatal conductance during the night, becoming to rise 3 h before dawn in olive cuttings of cv. Chemali de Sfax. In addition, the study of g_{night} and E_{night} by leaf-level gas exchange includes the loss across both cuticular and stomatal components (Caird et al., 2007). This limitation can be avoided by determining the cuticular transpiration ($E_{cuticular}$).

Nocturnal warming is likely to have a significant effect on respiration rate (R) (Catoni et al., 2013; Turnbull et al., 2002), especially on the maintenance component that, in opposite to growth respiration, increases exponentially with temperature (Peraudeau et al., 2015). As plant biomass production depends on the balance between A_N and R (Pérez-Priego et al., 2014), R is a determining factor to maintain growth and productivity, particularly in conditions in which A_N is negatively affected, such as under drought conditions (Flexas et al., 2005; Galmes et al., 2007; Ribas-Carbo et al., 2005). Although R usually presents an order of magnitude lower than A_N, photosynthesis is limited temporally, while R occurs continuously in different plant organs (Flexas et al., 2005; Galmes et al., 2007). Contrarily to the A_N response to drought, that is well investigated, the respiratory process has been commonly marginalized and the few information available tend to be contradictory. Apart to the trend, also the mechanisms underlying R regulation under drought are still largely unknown and most of the studies assessed R on darkened leaves during the day. However, these responses can differ at night, once may change substrate supply and sink demand compared with normal nocturnal conditions (Ribas-Carbo et al., 2005) and, because daytime and nighttime temperatures differ substantially. Improve the knowledge of the importance of R to plant carbon balance during water stress is the first step to enable prediction and management of crop growth and yields in water-stress-prone areas (Flexas et al., 2005). Moreover, may help to hypothesize more accurately species behavior under new climatic conditions (Varone and Gratani, 2015).

Therefore, we address the following questions: (1) It is E_{night} substantially higher than $E_{cuticular}$?; (2) If so, can different water regimes determine the occurrence and magnitude of g_{night} and E_{night}?; (3) Can leaf anatomical structure influence nighttime water balance?; (4) How R_{night} responds to different water regimes? (5) What are the most probable causes of g_{night} and E_{night}?; (6) What are the implications and opportunities of g_{night} and E_{night} to olive tree?

2. Material and methods

2.1. Plant material and growth conditions

The experiment was carried out with own-rooted 3 years-old olive trees (*Olea europaea* cv. Cobrançosa), between June and September 2014 at the University of Trás-os-Montes and Alto Douro, Vila Real, Northeast Portugal (41°17′17.83″N, 7°44′12.81″W, 448 m a.s.l.). Plants were grown outdoors in 16 l pots containing a mix of sandy-loam soil and horticultural substrate Siro Oliva (Siro-Leal & Soares SA, Mira, Portugal) (2:1). The surfaces of containers were covered with a thin layer of perlite and sealed with plastic film and aluminum foil. This measure aimed to avoid the evaporation from soil surface and the rain water entering to the pots, and to minimize the temperature increase inside the containers. Pots were randomly arranged and periodically rotated to the neighboring position to minimize the effects of environmental heterogeneity. When applicable, plants were watered to field capacity, determined gravimetrically. Care was taken to ensure negligible leaching through the bottoms of the containers during irrigation. All the plants were manually defruited immediately after fruit set to avoid yield influences on the measured variables.

The climate of the study site is typically Mediterranean-like, a warm-temperate climate with dry and hot summers, classified as Csb according to Köppen-Geiger's classification. Mean annual rainfall is 1023 mm, most of which falls in the autumn-winter with negligible rainfall during the summer months, although 2014 was an atypical summer with some rainfall events. The warmest months are July/August and the coldest months are December/January, with mean daily temperatures of 21.3/21.7 °C and 6.8/6.3 °C, respectively (IPMA, 2017). The climatic conditions during the field measurements are presented in Fig. 1.

2.2. Experimental plan

Forty uniform selected plants, based on height, leaf number and leaf area were submitted to an acclimatization period of 30 days. At the beginning of the experiment, 6th July, eight plants randomly chosen were harvested to assess the initial biomass of the different plant organs. The remaining thirty-two plants were divided in two groups, each one comprising sixteen plants. One group was kept under well-watered conditions (WW, control plants) throughout the entire experimental period, in which plants were watered every day. The other group was subjected to three "drought-re-watering cycles" (WS, stressed plants) by withholding water until the occurrence of precipitation (1st and 2nd cycles), or until the stomatal conductance for water vapor (g_{day}) during mid-morning (peak of photosynthetic activity) dropped around 50 mmol m^{-2} s^{-1} (reached at 3rd cycle), a threshold value indicating a situation of severe drought stress experienced by the plants, at that value photosynthetic activity becomes predominantly inhibited by metabolic processes, besides stomatal limitations (Flexas and Medrano, 2002). When occurred precipitation, or when olive trees reached the desired drought intensity, they were re-watered to field capacity in the evening and also during the following days until A_N was almost restored to control values (recovery). The 1st, 2nd and 3rd "drought-re-watering cycles" had the duration of 12-6 days, 9–3 days and 21–16 days, respectively.

Each group of sixteen plants was divided in two subgroups, each one with eight plants arranged in a completely randomized design with four replications (two plants per experimental unit). Plants from one