



## Responses of transpiration and transpiration efficiency of almond trees to moderate water deficits



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### ABSTRACT

The majority of world almond acreage is grown under rainfed conditions but most of the production is obtained under irrigation. Increased water scarcity is reducing water availability for irrigation thus the need to characterize the responses of almond to water deficits. Several works have defined well the stomatal closure in almond leaves under water deficits, but the behavior at the canopy level is not well understood. A field experiment was conducted in an almond (cv. Guara) orchard in Córdoba (Spain) under four different levels of irrigation supply to investigate the responses of almond tree transpiration (T) and transpiration efficiency (TE) to water stress. Stem water potential ( $\Psi_x$ ), whole tree transpiration (T) and leaf gas-exchange were periodically measured throughout the 2013 growing season. Tree T decreased linearly as midday  $\Psi_x$  decreased below a threshold value of about  $-1.1$  MPa, and declined to about 50% of the Control value when midday  $\Psi_x$  reached  $-1.6$  MPa. The quick decline in T in response to the lowering of  $\Psi_x$  suggests a high sensitivity of almond T to water deficits. The instantaneous transpiration efficiency (TE) of almond leaves was unaffected by water and varied essentially with vapor pressure deficits. On a daily scale, the leaf TE of stressed trees followed the same pattern as in the non-stressed trees. Then, contrary to the behavior observed in olive and citrus, there were no instantaneous or daily TE increments in almond trees in response to water deficits.

### 1. Introduction

World almond production is on the increase (FAOSTAT) in response to an increase in demand due to its nutritional qualities (Jenkins et al., 2002; Berryman et al., 2011). Although almost 70% of production takes place under irrigation (FAOSTAT, 2014), there are large areas in Mediterranean countries where it is grown rainfed or under very limited irrigation (those areas represent about 75% of almond world cultivated area). Almond trees adapt well to drought conditions by combining stomatal control of transpiration with hastened leaf senescence when subjected to water deficits. At the leaf level, stomatal closure in almond in response to water deficits has been widely documented (Castel and Fereres, 1982; Torrecillas et al., 1988; Marsal et al., 1997; Shackel, 2007). A general conclusion of these studies is the gradual reduction of stomatal conductance ( $g_s$ ) in the deficit treatments compared to well-irrigated which was attributed to a decrease in leaf water potential ( $\Psi_l$ ). However, stomatal behavior is complex and responds also to other factors (light intensity, vapor pressure deficit,  $CO_2$

concentration, etc.), thus the association between  $g_s$  and  $\Psi_l$  is clearer when water stress is severe and plant water status had a dominant role in controlling stomatal function (Torrecillas et al., 1988; Romero and Botía, 2006). Shackel (2007) reported a reduction of 50% in  $g_s$  when stem water potential ( $\Psi_x$ ) was  $-1.4$  to  $-1.8$  MPa, a level of water stress that may be considered moderate for almond, as values as low as  $-4.0$  MPa have been reported for severe stress levels (Castel and Fereres, 1982). Other authors have shown that the degree of stomatal closure in response to water deficits varies among different cultivars (Torrecillas et al., 1996; Rouhi et al., 2007; Yadollahi et al., 2011). Studies aimed at developing regulated deficit irrigation strategies in almond have also reported reductions in  $g_s$  (Hutmacher et al., 1994; Goldhamer and Viveros, 2000; Romero et al., 2004; Romero and Botía, 2006). All these works measured  $g_s$  decreases in deficit irrigation treatments compared to control. For instance, Romero et al. (2004) found a decrease of 67% of  $g_s$  at maximum stress. Hutmacher et al. (1994) and Romero et al. (2004) reported the seasonal course of  $g_s$ , measured as water deficit developed. They observed that the decrease

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occurs early and gradually during the season, and that it was closely related to  $\psi_1$  decrease.

Although, the responses of almond trees to water deficits have been widely studied at the leaf level, little is known about how whole trees react to water stress. We hypothesize that the reduction in  $g_s$  measured in almond at the leaf level, should be translated into less water transpired by the tree at the canopy level. It is in agreement with the previously estimated high degree of coupling between the leaves of tree canopies, such as almonds, and the atmosphere (Jarvis, 1985). In such cases, transpiration is driven by the atmospheric saturation deficit and strongly regulated by stomatal conductance, thus a certain level of stomatal closure is translated into about the same level of tree transpiration reduction (Jarvis and McNaughton, 1986; Fereres et al., 2014). Consistent with that view, Phogat et al. (2013) measured a reduction in almond root water uptake of 146 mm in a deficit irrigation (DI) treatment (65%  $ET_c$ ) than under full irrigation (FI) in an experiment with almond cv. Nonpareil. Unfortunately, in most other almond DI studies (Girona et al., 2005; Goldhamer et al., 2006; Egea et al., 2010, 2013; Stewart et al., 2011)  $ET$  or  $T$  were not measured, and the authors refer to “water savings” in deficit treatments as reductions in applied irrigation water, without quantifying the contribution of stored soil water to  $ET$ . In some cases, (i.e., Goldhamer et al., 2006), due to the low soil storage capacity and lack of rainfall, it can be inferred that there must have been reductions in  $ET$  in the stressed treatments, as the contribution of water from the soil reserves is small as compared to total crop water requirements. By contrast, a recent study (Spinelly et al., 2016) reported that, even though stomatal closure was detected, orchard  $ET$  measured by eddy covariance did not decrease under moderate water deficits. Therefore, there is still the need to quantify the whole tree responses of transpiration under water deficit conditions.

At the leaf level, water loss and  $CO_2$  gain shares the same path through the stomata, the fluxes being driven by the corresponding concentration gradients between in and out of the leaf. The regulation of carbon gain ( $A$ ) in relation to water loss ( $E$ ) at leaf level has been the subject of in-depth analyses by Cowan and Farquhar (1977) and Cowan (1982), among many others. High values of VPD will increase the  $H_2O$  gradient and then  $TE$  will be lower than for low VPD values, as  $CO_2$  gradient is relatively constant. Here the question arises of whether the ratio of  $CO_2$  assimilation to water transpired in almond, termed transpiration efficiency ( $TE$ ) increases under water stress as it has been observed in other tree species. Such an increase, if scaled up to whole tree  $T$ , should lead to favorable tree responses to DI. Studies in olive trees by Villalobos et al. (2012) found that there were only slight improvements of the instantaneous  $TE$  in stressed trees. However, when  $TE$  was integrated over the diurnal cycle, it was significantly higher in stressed than in well irrigated trees. This was explained by a displacement of the pattern of gas exchange of the stressed trees towards the early morning hours when VPD is still low. At midday, when VPD is high, stomata of stressed trees were fully closed while there was some gas exchange in the irrigated trees leading to low  $TE$ . A similar, although less pronounced, behavior has been documented by Rocuzzo et al. (2014) in orange trees. Even though there were no differences in instantaneous  $TE$  between stressed and non-stressed orange trees, the stressed trees exhibited greater  $TE$  on a daily basis. In both species, the positive  $TE$  response to water stress favors the application of deficit irrigation strategies (Rocuzzo et al., 2014).

In almond, very few and inconclusive studies have documented the responses of leaf level  $TE$ . Klein et al. (2001) and Romero et al. (2004) measured lower values of  $TE$  in stressed than in full irrigated almond trees (cv. Non-pareil). By contrast, Romero and Botía (2006) found that mean daily  $TE$  was higher in the deficit treatments than in the control, due essentially to differences of instantaneous  $TE$  during the early hours of the morning. In another field study, Egea et al. (2011) did not find changes in  $TE$  when water stress was imposed on almond trees by partial root drying.

Considering the actual trend of increasing the almond acreage

especially in semi-arid conditions (in some cases at the expense of well-adapted deficit irrigated Mediterranean species, such as olive), it is of foremost importance to increase our knowledge on the water use by this crop, especially under water stress situations. The objectives of this study were 1) to investigate the responses of whole tree transpiration to moderate water deficits; and, 2) to determine whether almond transpiration efficiency is enhanced by water stress.

## 2. Materials and methods

### 2.1. Description of the site and experimental setup

The study was conducted during 2013 in an almond orchard located at the Research Center of IFAPA-Alameda del Obispo, in Cordoba, Spain (37,8°N, 4,8°W). The almond trees [*Prunus dulcis* (Mill.) D.A. Webb cv. Guara, grafted on G677 rootstock] were planted in 2009 at a spacing of 6 m × 7 m. The climate at the site is Mediterranean with hot and dry summers and mild winters, and 600 mm annual precipitation. The soil of sandy loam texture is deep, of alluvial origin, and is lighter below the 150 cm depth; the upper and lower limits of soil water storage are 0.23 and 0.08 cm<sup>3</sup>/cm<sup>3</sup>, respectively. The trees were fully irrigated since planting until the start of the experiment in 2013. Trees were daily irrigated with a compensated drip system, with 12 emitters (2,4 l/h) per tree. During the spring of 2013 rainfall was exceptionally high, totaling 383 mm during the months of March, April and May, which is more than twice the average and largely exceeded  $ET_c$  (72.8 mm). Therefore, irrigation did not start until mid-June.

The irrigation season started on 15th June and ended on 11th October. Fully irrigated treatment received the equivalent of  $ET_c$ , calculated following Fereres et al. (2012) as  $ET_o \times K_c$  times a reduction coefficient based on canopy size ( $K_{r,c}$ ). The  $ET_c$  of a tree measured in a weighing lysimeter located in the same field (Espadafor et al., 2015) was used to adjust the calculated irrigation amounts in the fully irrigated plots. Climatic data for the calculation of  $ET_o$  were collected from an automated weather station located over grass which was about 300 m apart from the orchard.

In 2013, this experiment was conducted within the orchard in which different irrigation levels were applied to trees from full irrigation to rainfed conditions. The experimental units used in the orchard had 16 trees out of which the four central trees were used for measurements and the rest as borders.

For the experimental results reported herein, we chose the following: a control treatment that received full irrigation (FI) requirements; a moderate deficit irrigation treatment (MS) that received 55% of the total amount of water applied to FI; a more severe deficit irrigation treatment (SS) that received 40% of the total amount applied to FI and a rainfed treatment that did not receive any irrigation (RF). We selected one of the central four trees from a plot of the FI, MS and SS treatments, and two central trees from a RF plot. The reasoning for selecting two rainfed trees was the higher variability in the response of the trees to water stress expected when the soil reserve became the only source of water. Therefore, in this study, the experimental unit was the tree.

### 2.2. Soil water measurement

Soil water content in the first 210 cm of soil profile was measured every 10 days with a neutron probe (Campbell Pacific Nuclear Scientific, Model 503). Eight aluminum access tubes were installed near the trunk of the selected trees, except for the rainfed trees where nine access tubes were placed covering the area between the two trunks. The neutron probe was calibrated for our soil characteristics using soil samples for gravimetric moisture content which were taken at the time of access tubes installation. Readings were taken at 30 cm intervals down to the 210 cm depth except for the first two readings, taken between 0 and 15 cm and 15–30 cm. Total soil water content down to the

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