



# Water stress causes stomatal closure but does not reduce canopy evapotranspiration in almond



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## ARTICLE INFO

### Article history:

Received 23 April 2015

Received in revised form 3 January 2016

Accepted 8 January 2016

### Keywords:

Stomatal conductance

Photosynthesis

Stem water potential

Crop coefficient

Canopy conductance

Eddy covariance

## ABSTRACT

We investigated the degree of physiological control of transpiration at the leaf and canopy-level in commercial almond orchards in California during periods of water stress ranging from  $-0.8$  to  $-2.0$  MPa of stem water potential. Field measurement of evapotranspiration using the residual of the energy balance method failed to detect a decrease of actual evapotranspiration ( $ET_a$ ) relative to standardized reference evapotranspiration for short canopies ( $ET_o$ ) during weekly periods of water stress. Although a decline in the ratio  $K_a = ET_a/ET_o$  is expected in presence of water stress as a result of stomatal regulation, a flat response to water stress was observed for both daily and average midday  $K_a$ . A substantial decrease in  $K_a$  was observed after harvest, perhaps caused by the decrease in leaf area resulting from harvest operations. Weekly cycles of irrigation caused a clear reduction in midday stem water potential, a sensitive indicator of water status in plants. At the leaf level, there was a continuous decline in stomatal conductance with declining stem water potential for both sunlit and shaded leaves. Shaded leaves had lower conductance values and a flatter slope than sunlit leaves. The results suggest that a decrease in conductance of roughly 50% is expected at the leaf level for the observed range of stem water potential. A scaling-up exercise together with a model of the energy balance indicated the expected magnitude the reduction in  $K_a$  for the observed range of stem water potential but did not account for the apparent disconnect between the leaf scale and the canopy scale. Our results underscored the complications associated with estimating plant water stress by measuring field evapotranspiration, especially when grass  $ET_o$  is used as the reference. From a water management point of view, this study suggests that inducing mild to moderate water stress in almond may not produce substantial water savings.

Published by Elsevier B.V.

## 1. Introduction

Almonds are one of the most important agricultural crops in California and a major player in the water budget of the state. Irrigation water is a limiting factor in the Southern San Joaquin Valley, where some farmers received only 20% of their normal water allocation in 2013. In tree crops, mild water stress can be intentionally induced to control excessive vegetative growth (Chalmers et al., 1981) and regulated deficit irrigation can be applied to conserve water (Romero et al., 2004; Girona et al., 2005; Goldhamer et al., 2006). Additionally, in almond production, irrigation is commonly cut off to facilitate harvest and reduce incidence of fungal diseases (Teviotdale et al., 2001). Given widespread water stress due

to both drought and management practice, however, it is important to understand the physiological response and water use of almond orchards under different degrees of imposed water stress. This knowledge will help guide irrigation decisions and increase water use efficiency.

To perform photosynthesis, plants face an inexorable tradeoff between carbon assimilation and water loss. The two processes are inextricably linked because they share the same transport pathway, both at the leaf and the canopy scale. The first step of the pathway is quantified by stomatal conductance ( $g_s$ ) through the stomatal aperture to the surface of the leaf and the second step by aerodynamic conductance ( $g_a$ ) from the leaf surface to the atmosphere surrounding the leaf. Stomatal conductance is under physiological control, while aerodynamic conductance is a function of wind speed and leaf size. The same principles for leaf transpiration can be applied to a canopy in the commonly used “Big Leaf” approach. In the Big Leaf model, the first step of the pathway is represented by canopy conductance ( $g_c$ ), a composite function of stomatal conductance,

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leaf area, and soil conductance (Kyaw Tha Paw and Meyers, 1989). Aerodynamic conductance is then modeled as a function of wind speed and canopy characteristics, i.e., height and roughness. (Allen et al., 1998).

Plants physiologically respond to mild water stress with stomatal closure, which reduces stomatal conductance over a short response time (Hsiao, 1973). Stomatal closure resulting from water stress has been shown in almonds (Torrecillas et al., 1996). However stomatal conductance also responds to environmental factors. It is affected by light intensity, possibly modified by the severity of water stress (Jones, 1992, p. 148). In general, decreased stomatal conductance should correspond to decreased canopy conductance, even though each leaf in a canopy is differently oriented and hence experiences different light intensity. Thus, the quantitative aggregate response to water stress of total canopy conductance is a function of the relative contributions from a leaf population experiencing a range of light intensities in a rather complex arrangement. Severe stress advances and accelerates leaf senescence (Bradford and Hsiao, 1982), which reduces leaf area and thus canopy conductance over a significantly longer response time. Therefore, physiological response to water stress should decrease canopy conductance and hence canopy water loss. However, some studies reported that canopy conductance does not depend entirely on physiology, vegetation and soil, but also on non-physiological variables (Baldocchi et al., 1991; Todorovic, 1999), although the influence of some of these variables may depend on the level of coupling (Jarvis and McNaughton, 1986; Moreno et al., 1996).

The relative importance of  $g_a$  and  $g_c$  determines the degree to which a canopy is “coupled” to the atmosphere and how much a proportional decrease in canopy conductance will decrease plant transpiration (Jarvis, 1984). A “decoupled” canopy can minimally control its transpiration rate via stomatal regulation, because the stomatal resistance is relatively unimportant compared to the larger aerodynamic resistance. The role of aerodynamic conductance in determining the sensitivity of transpiration to stomata is well known (Bange, 1953). Jarvis (in Grace et al., 1981) showed the same results for canopies, suggesting that tall canopies such as forests show high canopy conductance and a coupled canopy. In contrast, short canopies like field crops have low aerodynamic conductance and are decoupled. Such a mechanism is less important for carbon assimilation rate because the canopy has a smaller influence on air  $\text{CO}_2$  than it has on air vapor pressure (Steduto and Hsiao, 1998b). Thus, in a decoupled canopy, stomatal closure may restrict photosynthesis more than it restricts transpiration.

The relative importance of carbon assimilation and water loss has been termed “water use efficiency” (WUE), and it is assessed using measures such as carbon assimilation/transpiration (Tanner and Sinclair, 1983), photosynthetic rate per stomatal conductance (Lambers et al., 2008, p. 53), and yield per irrigation water applied in deficit irrigation practices (Goldhamer et al., 2006; Chalmers et al., 1986). It is generally accepted that water stress, by inducing stomatal closure, increases water use efficiency, however Rouhi et al. (2007), in different almond species, showed contrasting patterns depending on the species. The potential for water conservation is greater in tree crops, since they are more coupled to the atmosphere than short, smooth canopy field crops (Ferreira and Soriano, 2007). The degree of coupling helps determine the water use efficiency when trees are under water deficit.

Irrigation scheduling is commonly managed using a soil water balance approach, where inputs are rain and irrigation and the most important output is crop evapotranspiration ( $ET_c$ ). The most common method is to estimate  $ET_c$  using a reference  $ET$  ( $ET_o$ ) and calculate  $ET_c$  as:

$$ET_c = ET_o K_c \quad (1)$$

where  $K_c$  is an experimentally determined “crop coefficient” (Allen et al., 1998). It is assumed that the  $ET_o$  represents a large field of 12 cm tall vegetation that is only limited by weather conditions. A modified Penman–Monteith (PM) equation based on generally accepted environmental physics theory and weather station measurements is used to determine  $ET_o$  (Allen et al., 1998, 2006). The  $ET_o \times K_c$  approach assumes a simple proportionality of  $ET_c$  to  $ET_o$ ; however, this approach may be too simplistic because  $K_c$  is highly dependent on the local climate and agronomic practices (Allen et al., 1998).

Annandale et al. (1994) criticized the  $ET_o \times K_c$  approach, that is based on the assumption of a simple linear relationship between  $ET_c$  and  $ET_o$ . In their study, they show that environmental factors affect grass  $ET$  differently than crop  $ET$ , particularly when the crop is tall and when canopy conductance is low due to ample irrigation. The  $ET_o \times K_c$  approach is commonly used due to widespread availability of  $K_c$  values for various crops in the literature (Doorenbos and Pruitt, 1977; Allen et al., 1998). In theory,  $K_c$  should be relatively stable in the short term, following a developmental pattern which is mainly affected by canopy growth and crop phenological stage and does not account for crop water stress. In the following equation,  $ET_a$  is the actual evapotranspiration of a crop, as opposed to  $ET_c$  that represents the potential unstressed crop  $ET$ :

$$ET_a = ET_o K_a \quad (2)$$

where  $K_a = ET_a/ET_o$  is the actual crop coefficient and describes the combined contribution of crop characteristics and crop stress.

An eddy covariance system (Burba, 2013) is often used to measure  $LE$ , but this method requires specialized personnel and expensive instruments that mostly limit it to research applications. This method has proven consistent with other measures of  $ET_a$  such as lysimeters (Castellví and Snyder, 2010; Alfieri et al., 2012). Thus, decreased canopy conductance due to water stress should reduce  $ET_a$  relative to  $ET_o$  and  $K_a$  relative to  $K_c = ET_c/ET_o$ , where  $ET_c$  is the crop evapotranspiration under standard conditions.

An alternative approach is to time irrigation based on plant water status as indicated by measuring midday stem water potential ( $\Psi_{\text{stem}}$ , Shackel, 2011), where  $\Psi_{\text{stem}}$  is closely associated with physiological and production parameters such as stomatal closure, photosynthesis, yield, and fruit quality (McCutchan and Shackel, 1992; Shackel et al., 1997; Naor et al., 2000). According to a recent Almond Board of California survey,  $\Psi_{\text{stem}}$  is currently being used as an irrigation management tool by 40% of almond growers.

This study aims to test the following hypothesis:

If a measurable reduction in stomatal conductance results from moderate to severe water stress that develops under standard commercial practices, and if such a reduction aggregates to a measurable decline in canopy  $ET_a$ , then  $ET_a$  should decrease relative to  $ET_o$  and the ratio  $K_a = ET_a/ET_o$  should decrease during water stress.

## 2. Methods

### 2.1. Experimental site

The experiment was conducted during 2008 through 2011 on a high-yielding (Schellenberg et al., 2012) almond (*Prunus dulcis* D.A. Webb) orchard at the Paramount Farming Company in the southern San Joaquin Valley near Lost Hills (N 35°30'37" W 119°40'3"). The almond cultivars were ‘Nonpareil’ (50%) inter-planted with ‘Monterey’ (50%), grafted on Nemaguard rootstocks (*Prunus persica*). Trees were planted in 1999 with 6.4 × 7.9 m spacing (213 trees ha<sup>-1</sup>), with a north-south row orientation on a Milham sandy loam (Fine-loamy, mixed, superactive, thermic, Typic Haplargids). Micro-irrigation was applied with two static fan-jet 4 L h<sup>-1</sup> microsprinklers per tree that were located north and south of each

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