

Combining a Process-Based Model of Stomatal Conductance with Leaf Turgor Pressure Related Probe Measurements to Study the Regulation of Plant Water Status and Stomatal Conductance under Drought

Rodríguez-Dominguez CM^{1,2}, Buckley TN³, de Cires A², Fernández JE¹, Pérez-Martin A¹, Díaz-Espejo A¹

1 Irrigation and Crop Ecophysiology Group, Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS, CSIC). Avenida Reina Mercedes 10, 41012 Sevilla, Spain. crdominguez@us.es

2 Departamento de Biología Vegetal y Ecología, Universidad de Sevilla, Sevilla, Spain

3 IA Watson Grains Research Centre, Faculty of Agriculture and Environment, The University of Sydney, Narrabri, NSW 2390 Australia

* e-mail: crdominguez@us.es

ABSTRACTS

The recently developed plant sensor of relative changes in leaf turgor pressure (LPCP probe) was compared with the turgor pressure output simulated with a process-based stomatal model (BMF model). Our results confirm the good agreement between the simulated turgor pressures and those derived from LPCP readings. The combined use of the BMF model and LPCP probes raised new insights into the regulation of hydraulic conductivity and osmotic pressure.

INTRODUCTION

The use of plant-based sensors is in many cases the recommended option for precision irrigation in horticultural crops since plants are an integral component of the soil-plant-atmosphere continuum (Jones, 2004). The output of the recently developed leaf patch clamp pressure probe (LPCP probe) targets on turgor pressure (Rüger *et al.*, 2010), one of the physiological variables recognized to be among the most sensitive to water stress (Jones, 2004). Process-based models have been also suggested as powerful tools to improve our understanding of plant physiological mechanisms involved in the response to water stress (Buckley & Mott, 2013). Our main objectives were (i) to assess whether the diurnal leaf turgor pressure changes derived from LPCP outputs agrees with absolute changes in leaf turgor pressures modeled by the BMF model (Buckley *et al.*, 2003) and (ii) to understand mechanisms of stomatal conductance regulation under water stress.

MATERIAL AND METHODS

The experiment was conducted in June 25 and August 3 of 2012 in a commercial hedgerow olive orchard (1667 tree ha⁻¹) near Seville, Spain. Sunny and shaded leaves were used to explain the physiological basis in the response of LPCP probes observed in a wide range of values in two irrigation treatments (one tree per treatment): well watered (WW), with daily irrigation to replace 100 % of the maximum potential crop evapotranspiration (ET_c); and

water stressed (WS), with a total of 30 % ET_c (details are given in Fernández *et al.* –2013–). Leaf water potential (ψ_{leaf}) and stomatal conductance (g_s) were measured diurnally every 1.5 hours with a Scholander-type pressure chamber (PMS Instrument Company, Albany, Oregon, USA) and a Li-6400 (LI-COR, Lincoln, NE, USA) with a 2 × 3 cm standard chamber, respectively. Relative changes in leaf turgor pressure were derived from *in situ* measurements with the non-invasive, online-monitoring LPCP probe (ZIM Plant Technology GmbH, Hennigsdorf, Germany). Relative leaf turgor pressure is determined by measuring the output leaf patch pressure, P_p , upon application of a constantly kept external magnetic pressure (P_{clamp}). The attenuation of the applied external pressure and thus P_p depends on the magnitude of the turgor pressure of the leaf (P_c) which is opposed to P_{clamp} (details are given in Rüger *et al.* –2010– and Ehrenberger *et al.* –2012–). Three LPCP probes per canopy position were installed (clamping procedure in Fernández *et al.* –2011–). To allow average the three LPCP probes of each position and comparison among them, a normalizing procedure of P_p (P'_p) was carried out:

$$(1) \quad P'_p = \frac{P_p - P_{min,1}}{P_{max,1} - P_{min,1}}, \text{ where } P_{min,1} \text{ is the minimum value (maximum turgor pressure)}$$

reached at pre-dawn of the decided experimental day (1 = June 25; 2 = August 3) and $P_{max,1}$ is the maximum value (minimum turgor pressure) reached during the same day.

We used a simplified version of the stomatal conductance model originally presented by Buckley *et al.* (2003) (BMF model) to derive leaf turgor pressure for assessing LPCP probes measurements:

$$(2) \quad g_{s,model} = \frac{\chi\beta\tau K(\Psi_s + \pi)}{K + \chi\beta\tau VPD}, \text{ where } K \text{ is leaf-specific hydraulic conductance, } \chi \text{ is a}$$

proportionality factor that includes effects of stomatal density, β is a parameter that describes sensitivity to epidermal turgor and ATP concentration, τ is ATP concentration in photosynthesising cells, Ψ_s is soil water potential, π is bulk leaf osmotic pressure and VPD is air vapour pressure deficit. The model assumes that the resistance from epidermal to guard cells is negligible compared to the resistance from the soil to the epidermis, and epidermal and bulk leaf osmotic pressure are similar. Variable hydraulic conductance (K_{var}) was obtained by fitting g_s data to the BMF model at single measuring time solving Equation (2) as:

$$(3) \quad K_{var} = \frac{g_s VPD}{\Psi_s + \pi - \frac{g_s}{\chi\beta\tau}}.$$

The modeled leaf turgor pressure (P_{model}) was derived from: $P_{model} = \Psi_{1,model} + \pi$, where $\Psi_{1,model}$ is the modeled leaf water potential estimated as:

$$(4) \quad \Psi_{1,model} = -\left(\frac{g_{s,model} VPD}{K} - \Psi_s\right), \text{ and } \pi \text{ is the maximum value estimated as:}$$

$$(5) \quad \pi = \frac{g_s}{\chi\beta\tau} - \Psi_{\text{leaf}}.$$

RESULTS AND DISCUSSION

In this study, we have found a good agreement between the output leaf patch pressure (P_p) and the turgor pressure estimated by the BMF model. This relationship was explained by a power function (Fig. 1) due to losses of the external clamped pressure applied to the leaf, which are theoretically embedded in the term leaf-specific attenuation factor (Ehrenberger *et al.*, 2012). We found a shift toward a more positive value of turgor for leaves of the WS treatment. We think that the most likely reason for explaining the difference between both treatments is related to the model output. Modeled turgor for the WS leaves was higher than that of the WW (Fig. 1D), which makes not much sense. The origin of the wrong performance of the BMF model might be due to the assumption of a constant π along the day. The existence of an active osmotic adjustment was evident not only in a diurnal basis. Seasonally our results suggest an increase in π leading to the shift toward more negative values of Ψ_{leaf} in its relationship with P_p (Fig. 2). The increase in π allows leaves to maintain turgor pressure at lower Ψ_{leaf} . If this hypothesis is correct, it would suggest as well that the hysteresis found in August in the WS leaves (Fig. 2B, D) was a consequence of the likely diurnal adjustment of π previously mentioned. The results of this study have awarded us not only on the need of using a dynamic parameter π in the BMF model, especially under water stress. Despite of the satisfactorily simulation by the BMF model of g_s (Fig. 3), the model was not able to interpret some points at the onset and end of the day (e.g. Fig. 3A). To account for these discrepancies, we evaluated a dynamic diurnal variation in K (K_{var}) as a possible physiological mechanism not considered in the model at its previous version. When the results were plotted as a function of Ψ_{leaf} (Fig. 4), we obtained a relation similar to that reported recently for olive leaves (Torres-Ruiz *et al.*, 2013). This suggests that K is also a highly dynamic parameter during the day and should be considered so for an adequate use and interpretation of model outputs.

CONCLUSIONS

The present research has confirmed the potential of the LPCP probes as tools for an automatic monitoring of leaf turgor pressure under field conditions. The combined use with the BMF model highlights the importance of considering in the future the dynamics of leaf osmotic potential and hydraulic conductance, both at a seasonal and daily scale.

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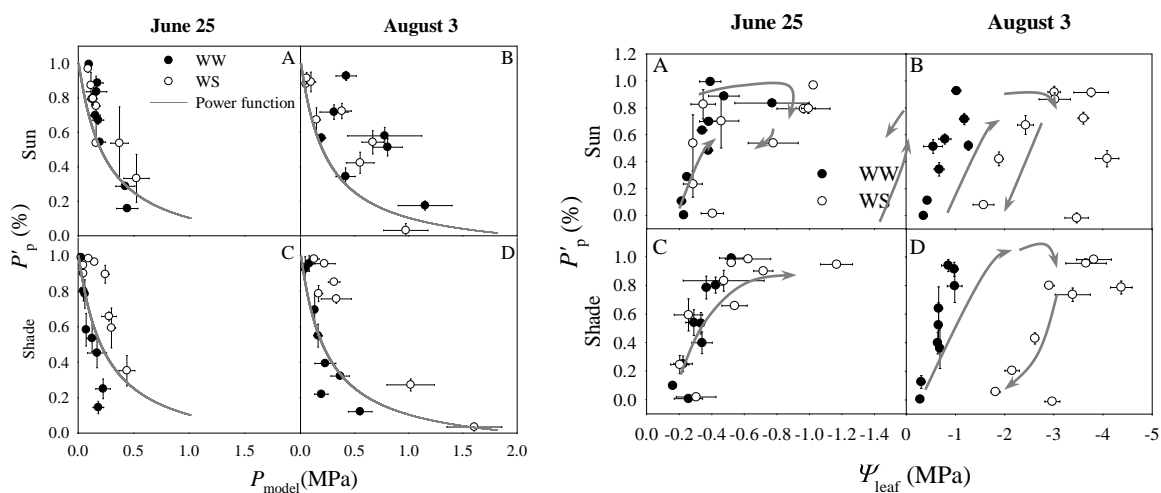


Figure 1 (left). Relationships between the normalized output leaf patch pressure (P'_p , %) and the absolute leaf turgor pressure modeled with the BMF model (P_{model}) on the two experimental dates in sunny and shaded leaves and for the two water treatments (WW and WS). Points are mean and error bars are standard errors for $n = 3$. Power function (gray line) is according to Ehrenberger *et al.* (2012).

Figure 2 (right). Relationships between the normalized output leaf patch pressure (P'_p , %) and the leaf water potential (Ψ_{leaf} , -MPa). Gray arrows indicate the diurnal evolution of the measurements. Rest as in Fig. 1.

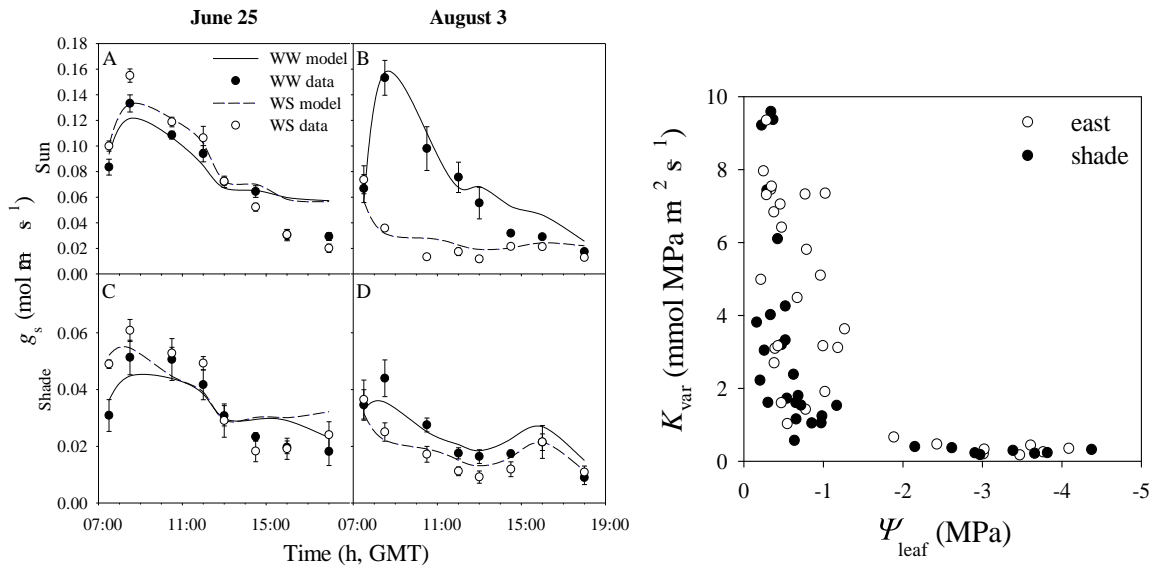


Figure 3 (left). Evolution of g_s data (points) and g_s fitted with the BMF model (lines). Rest as in Fig. 1 $n = 4$ for g_s data. GMT = Greenwich Mean Time.

Figure 4 (right). Diurnal variation of soil-to-leaf hydraulic conductance (K_{var}) plotted against leaf water potential (ψ_{leaf}) measured in sunny and shaded leaves and mixing the two water treatments and the two experimental dates. Each point represents the average of $n = 4$ (K_{var}) and $n = 3$ (ψ_{leaf}). Error bars are not presented for a clearer view of the figure.