# Using a process-based stomatal model in olive and its potential application to deficit irrigation studies

Rodriguez-Dominguez C.M.[1,2], Buckley T.N.[3], Fernández J.E.[1], de Cires A.[2], Rubio-Casal A.E.[2], Cuevas M.V.[1], Elsayed-Farag S.[1], Martin-Palomo M.J.[4], Muriel J.L.[5], Perez-Martin A.[1], Torres-Ruiz J.M.[1], Diaz-Espejo A.[1]

[1] Instituto de Recursos Naturales y Agrobiología (IRNAS-CSIC), Aptdo. 1052, 41080-Sevilla, Spain   crdominguez@us.es

[2] Departamento de Biologia Vegetal y Ecologia, Universidad de Sevilla, Sevilla, Spain

[3] Department of Biology, Sonoma State University, 1801 E Cotati Ave, Rohnert Park, CA 11 94928, USA

[4] ETSIA, Departamento de Ciencias Agroforestales, Universidad de Sevilla, Sevilla, Spain

[5] IFAPA, Centro Las Torres-Tomejil, Junta de Andalucía, Alcalá del Río, Sevilla, Spain

## ABSTRACT

Over the last years modeling plant transpiration has been pointed out as a powerful tool to optimize the management of irrigation in fruit trees. In this study we tested the hydromechanical model of stomata functioning proposed by Buckley et al. (2003), a model with a strong physiological basis. The great contribution of this model is that its parameters have direct physiological meaning. Firstly, the model was simplified to make its parameters estimation friendly and easy. Secondly, the model was fitted to data obtained in a hedgerow olive orchard under regulated deficit irrigation. The hydromechanical model fitted our data satisfactorily and allowed us to analyze the physiological parameters obtained.

## INTRODUCTION

Improvements in water use efficiency and precise irrigation scheduling are crucial in fruit trees orchards of arid and semi-arid environments where the water resource is scarce. Thus, there is a raising need to predict the consequences of drought on transpiration in crop plants, but especially to understand the mechanisms behind the main limitations to stomatal conductance. Under water stress conditions, modelling stomatal conductance is a key component of any model of plant transpiration. However, up to date, most of models used have failed to reproduce the effect of soil water deficit satisfactorily, and in the best of the cases they did it in a very empirical fashion. Buckley et al. (2003) proposed a hydromechanical model of stomata functioning which has been simplified to be friendly applicable in a hedgerow olive orchard under deficit irrigation. The aim of this work was to assess the applicability of the model under field conditions, and to evaluate the relative weight of hydraulic and non-hydraulic signals in the control of transpiration by stomata.

## MATERIAL AND METHODS

The experiments were made in the irrigation season of 2011 (from June to October) in a hedgerow olive commercial orchard (1667 trees ha$^{-1}$) located at 25 km to the west of Seville,

Spain. The 5-year-old 'Arbequina' trees were distributed in a randomized complete block experimental design with 4 plots per treatment. Meteorological variables were obtained from a weather station located in the orchard. From June 14, day of year (DOY) 165, to October 24 (DOY 297), two water treatments were imposed: a Control, in which the trees were daily irrigated to replace 100% of the irrigation needs; and a regulated deficit irrigation (RDI) treatment, in which the trees were irrigated to a total of 30% of crop evapotranspiration (30RDI). Soil water status was monitored 1-2 times per week with a Profile probe (Delta-T Devices Ltd, Cambridge, UK). Physical properties characterized the soil in two layers: a sandy loam layer for the first 0.6 m, and a sandy clay layer around 0.6 m and downwards. Leaf area, root area, plant water status, maximum stomatal conductance ($g_s$) and osmotic pressure ($\pi$) were monitored once every two weeks (more details in Diaz-Espejo et al., 2012). Transpiration was determined by the compensation heat pulse technique (Tranzflo NZ Ltd., Palmerston North, New Zealand) in three trees per water treatment. The resulting values of each set of probes, collected every 30 min, were averaged to derive the plant water consumption per leaf area ($E_p$, mmol m$^{-2}$ s$^{-1}$). Canopy conductance ($g_c$) was estimated as: $g_c$ = $E_p$/VPD, being VPD the air vapour pressure deficit and assuming a complete coupling between canopy and atmosphere (Jarvis and McNaughton, 1986). We simulated this variable as a surrogate of $g_s$ with the BMF model (Buckley et al., 2003). The model predicts $g_s$ as:

$$g_s = \frac{\chi(\beta\tau - M)(\Psi_s + \pi)}{1 + \chi(\beta\tau - M)RVPD}$$

that includes soil water potential ($\Psi_s$), leaf osmotic pressure ($\pi$), plant hydraulic resistance ($R$), evaporative demand (VPD), net epidermal mechanical advantage ($M$), a scaling factor that includes effects of stomatal density ($\chi$), a parameter that describes sensitivity to epidermal turgor and ATP concentration ($\beta$) and the concentration of ATP ($\tau$). The model assumes that guard cell osmotic pressure is a function of both epidermal turgor pressure and the concentration of ATP in photosynthesizing cells, and is actively regulated. $\Psi_s$, $\pi$ and VPD were measured and input to the model, $\chi\beta$ and $R$ were fitted by least squares as two individual parameters, and $\tau$ was simulated using the model of Farquhar and Wong (1984).

**RESULTS AND DISCUSSION**

Figure 1 shows a first period where all trees were daily irrigated (left panel) and a second period where 30RDI changed the irrigation frequency to once or twice per week. Despite variation in VPD, transpiration was steady during the first period, indicating strong stomatal regulation. $E_p$ dropped in 30RDI in the second period, exhibiting marked cycles of stress and recovery following irrigation events. These results were explained by the high percentage of sand in the soil and by the reduced and shallow rhizosphere of the young olive trees. The

BMF model fitted to the data satisfactorily in both treatments (Figure 2). As the soil dried out, differences emerged between treatments. Furthermore, $g_c$ values obtained were very similar to those estimated from leaf gas exchange, assuming a fraction of sunny leaf area between 0.2 and 0.3 (Moreno et al., 1996). The main advantage of the BMF model over most other mechanistic stomatal models is that it allowed us to analyze the physiological parameters obtained (Figure 3). Both Control and 30RDI trees had similar osmotic adjustment, despite of the difference in leaf water potential between both treatments. Reduced IAs and low irrigation frequency led to increase drastically the parameter $R$ fitted by the model in 30RDI trees. This high decrease of plant hydraulic conductivity should be explained due to an increase in $R$ in roots or leaves, since shoot have been reported to be resistant to cavitation at water potentials measured in this study (Diaz-Espejo et al., 2012). The second fitted parameter, $\chi\beta$, showed seasonal dynamics in both treatments. This parameter is related with the flux of ions entering the guard cells, responding to hormonal signals, like ABA, and controlling its turgor pressure. These results suggest that $\chi\beta$ is not only regulated by soil moisture, and hence, nor by ABA signals from droughted roots, so if ABA is involved its synthesis must be promoted by other environmental factor (like high VPD or oxidative stress in leaves).

**CONCLUSIONS**

We conclude that the use of a process-based stomatal model helped us to advance understanding of water use by an olive orchard planted in hedgerow. The BMF model predicted satisfactorily the actual canopy conductance, and hence, the actual transpiration. Both hydraulic and non-hydraulic signals were identified in the response to water stress. Hydraulic limitation played a major role when comparing water treatments.

**ACKNOWLEDGEMENTS**

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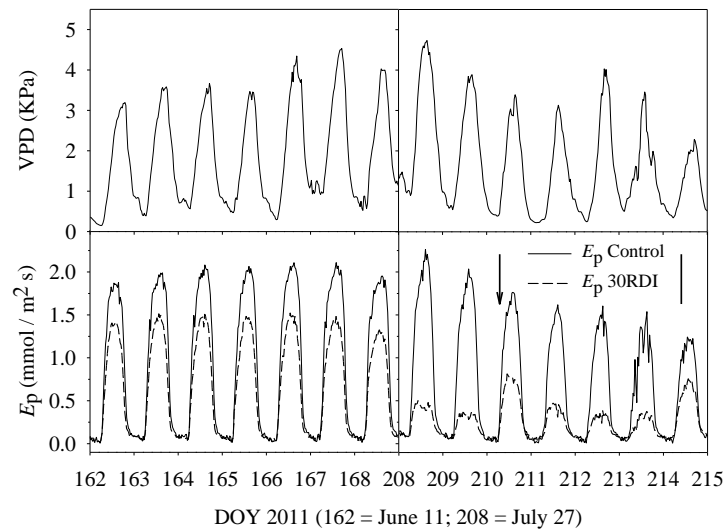Moreno et al. (1996). Transpiration and root water uptake … Plant Soil, 184: 85-96.

Figure 1. Time courses of evaporative demand (VPD) and transpiration estimated from sap flow measurements ($E_p$). Arrows: Irrigation events. DOY = Day of year.
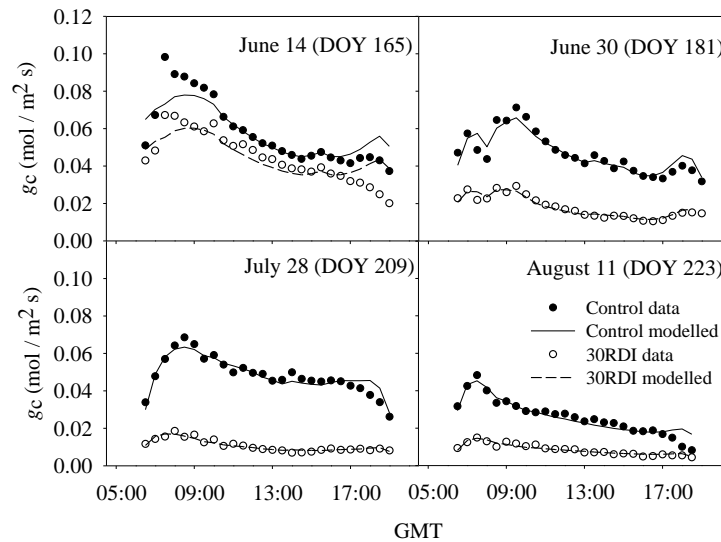


Figure 2. Evolution of canopy conductance ($g_c$) derived from sap flow measurements for both Control (close circles) and 30RDI (open circles) trees. Lines: Simulation of $g_c$ with the BMF model. Soil matric potential was estimated from $\Psi_{pd}$. GMT = Greenwich mean time.
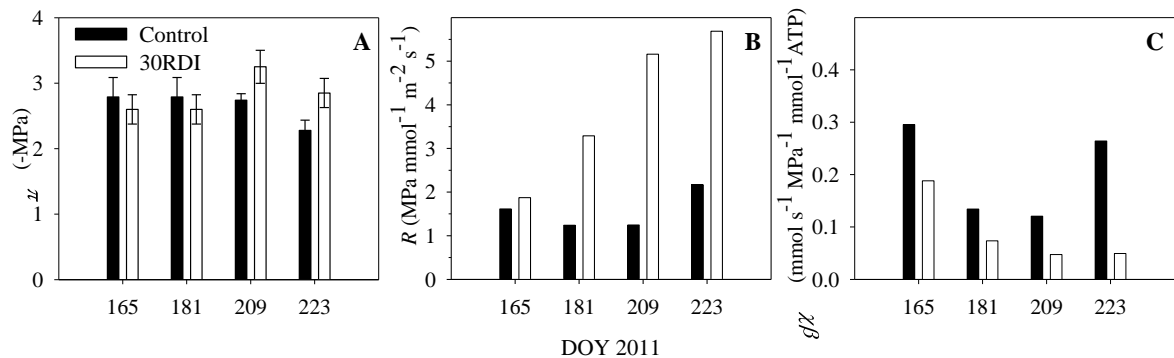


Figure 3. Seasonal evolution of the parameters derived from the BMF model. A) Measured osmotic pressure of leaves ($\pi$, n = 8). B) Soil-to-leaf hydraulic resistance (R). C) Sensitivity of the hydroactive mechanism of response of guard cells to turgor pressure, potentially related to ABA ($\chi\beta$).