



A model exploring whether the coupled effects of plant water supply and demand affect the interpretation of water potentials and irrigation management



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ABSTRACT

Water potential is a useful predictive tool in irrigation scheduling as it, or a component, is associated with physiological responses to water deficit. Increasing atmospheric *demand* for water increases transpiration and decreases water potential for the same stomatal conductance. However, based on *supply* by the soil-plant-atmosphere-continuum, decreasing soil water potential should decrease stomatal conductance and thus transpiration but also decrease water potential. Such contradictory behavior of supply and demand responses, may limit the value of water potential as an indicator of plant water status. This work studied the relationship between plant water potential and transpiration affected by supply (soil moisture) and atmospheric evaporative demand, and has implications for interpretation of water potentials and irrigation management. Results were that plant water potential has a narrow range of sensitivity to variation in supply and demand in hydrated soils, but greatly varying sensitivity in dry soils, limiting interpretation under dry conditions. Loss of soil conductance in dry, coarse soil types affects the trajectory of plant water potential response to supply and demand. Sapflow measurements on almonds indicated that variation in reference evapotranspiration and/or soil moisture deficit led to similar variation in stem water potentials to that predicted by the model. The model indicates hypotheses that with further testing may have important repercussions on the measurement of plant water use and irrigation scheduling.

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1. Introduction

The responses of plants to water stress modulate physiological processes such as carbon assimilation, growth, reproductive success and water uptake (Hsiao, 1973). Thus, our understanding of water stress has important implications for both physiological studies and practical applications such as irrigation scheduling.

Water potential (Ψ) is considered as particularly informative as it is related to many plant processes: it integrates the hydrostatic, gravitational, matric and osmotic effects on water availability. However, some authors have criticized the focus on Ψ , suggesting that relative water content or components of Ψ may be better indicators of physiological responses (Passioura, 1988; Sinclair and Ludlow, 1985). As relative water content measurements are prone to error (Arndt et al., 2015; Boyer et al., 2008), plant water potential has remained as a standard indicator of physiological and irrigation status. Leaf to leaf variability in water potential occurs due

to differences in orientation and boundary layer conductance, and therefore stem water potential (Ψ_{stem}) can be used as a more averaged and stable indicator of plant water stress (Choné et al., 2001; Marsal et al., 2005; McCutchan and Shackel, 1992; Naor et al., 1995). Stem water potential, measured using light, pump-up pressure chambers, is being used to schedule irrigation in fruit and nut tree horticulture in California, in particular by the large almond industry (Goldhamer and Fereres, 2001; Shackel, 2011)

However, Ψ as a stress indicator relates to the fact that responses to water stress such as stomatal closure, senescence etc., are regulatory mechanisms that control transpiration (T). Thus, a stress-related decrease in T may totally or partially maintain Ψ_{leaf} (or Ψ_{stem}) in a physiological range (Jones, 1983, 1990). The degree to which this homeostasis of Ψ occurs is thought to be species and variety-dependent leading some authors to define isohydric (with a stable Ψ_{leaf} and strong stomatal control) and anisohydric (variable Ψ_{leaf} with weak stomatal control) behaviors in response to variation in evaporative demand (Klein, 2014; Schultz, 2003; Tardieu and Simonneau, 1998). Although species may show behaviors that fall on the continuum between aniso- and isohydry, for many species water potentials can be used as a proxy for water

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Table 1
Variables and units used in the model.

Symbol	Quantity	Unit
b	Exponent of the soil moisture release equation	Unitless
C_p	Air heat capacity at constant pressure	$1204 \text{ J K}^{-1} \text{ kg}^{-1}$
e	base of the natural logarithm	2.71828 Unitless
e_a	Air vapor pressure	Pa
$e_{\text{sat}}(T_{\text{air}})$	Saturated vapor pressure at air temperature	Pa
g_a	aerodynamic conductance	m s^{-1}
g_c	canopy conductance	m s^{-1}
g_s	stomatal conductance	m s^{-1}
g_{sun}	stomatal conductance of sunlit leaves	$\text{mol m}^{-2} \text{ s}$
g_{shade}	stomatal conductance of shaded leaves	$\text{mol m}^{-2} \text{ s}$
G	Ground heat flux	W m^{-2}
K_a	Crop coefficient, ratio of actual to reference ET	Unitless
K_s	Soil saturated conductivity	$\text{W MPa}^{-1} \text{ m}^{-2}$
$K_{\psi(\text{soil})}$	Soil conductivity as a function of Ψ_{soil}	$\text{W MPa}^{-1} \text{ m}^{-2}$
LAI	Leaf area index	Unitless
LE	Transpiration or Latent heat flux	W m^{-2}
R_n	Net radiation	W m^{-2}
R_p	plant hydraulic resistance	$\text{W MPa}^{-1} \text{ m}^{-2}$
R_{soil}	soil hydraulic resistance	$\text{W MPa}^{-1} \text{ m}^{-2}$
R_{tot}	hydraulic resistance of the soil-plant system	$\text{W MPa}^{-1} \text{ m}^{-2}$
T_a	Air temperature	K
$T_{\text{air}}^{\circ}\text{C}$	Air temperature in Celsius	$^{\circ}\text{C}$
γ	Psychrometric constant	67 Pa K^{-1}
Δ	Slope of the vapor pressure and temperature relationship	Pa K^{-1}
ρ	Air density	kg m^{-3}
Ψ_e	Soil air entry value	MPa
Ψ_{soil}	Soil water potential	MPa
Ψ_{stem}	Midday stem water potential	MPa

status, while stomata also exert considerable control over water status (Tardieu and Simonneau, 1998). In the case of almond, stomatal conductance is consistently linearly related with stem water potential (Egea et al., 2011; Spinelli et al., 2016). For such species, the relationship of Ψ to T is the result of two opposite behaviors: first, a decrease in T is expected when Ψ decreases (more negative) due to stomatal closure under limited water supply; second, a drop in Ψ is expected as T increases due to increased demand. These two behaviors are the basis of a heuristic model developed here to test the conflicting influence of coupled supply and demand factors on transpiration and water potential. The impact of the canopy energy balance is likely to be particularly important to incorporate in the model, as changes in stomatal conductance would be somewhat counteracted by the response of increasing temperature (Table 1).

For the purposes of irrigation management, a proxy of the evapotranspiration of a crop (ET_c) can be calculated from multiplying the reference evapotranspiration for a grassy reference surface (ET_o) and the crop coefficient (K_c). The use of ET_o and ET_c assumes that the reference ET can be used to account for variation in evaporative demand when interpreting field transpiration data (Espadafor et al., 2013; Johnson et al., 2005; Williams et al., 2012). Similarly dividing an observed T by ET_o should detrend the T for variation in evaporative demand. However, ET_o is specifically for a grassy reference surface, not trees, and does not account for the feedbacks of Ψ on T and effects of soil moisture. Thus, the models developed below were also used to explore the effect of soil moisture and evaporative demand on the use of ET_o .

More broadly, this work is an attempt to capture the interdependence between transpiration and water potential in almonds, modelling the behavior of three interdependent variables (T, Ψ_{stem} and stomatal conductance) in a system of three equations/behaviors (Appendix A). The three behaviors are: T decreases as stomata close, modelled with Eq. (1); Ψ decreases with T

increases, modelled with Eq. (2); stomata close with decreasing Ψ_{stem} , based on an empirical relationship observed in almond (Spinelli, 2015). The model was run varying Ψ_{soil} and environmental variables affecting the evaporative demand of the atmosphere in order to mimic the natural conditions experienced by plants in the field. A validation of the model was attempted using sapflow velocity to estimate transpirational flow and measurements of Ψ_{stem} .

With the objective of investigating the validity of Ψ_{stem} as a predictor of T for almonds, this study explores the following questions through modelling and sap flow data:

- What is the relationship of T with Ψ during supply (soil) and demand (atmosphere) limitations? How does changing soil conductivity over a soil dry-down affect this relationship?
- Does stomatal conductance variation result in proportional variation in transpiration with soil drydown?
- Do the interrelated variables affect the usefulness of grassy reference surface ET_o in irrigation management for tree crops?

2. Model development: a hydraulic model of supply and demand influences on transpiration

The response of transpiration (T) to variation in Ψ due to changing atmospheric demand can be described using an energy balance approach that calculates transpiration as a function of atmospheric variables and stomatal conductance, under the assumption that stomatal conductance has a monotonic relationship with Ψ (in the leaf or any other part of the plant) (Fig. 1). Thus the demand side response of canopy T to water potential can be modelled based upon the Penman-Monteith equation (Monteith and Unsworth, 1990), based upon the assumption that a mature almond orchard soil evaporation is low (see Appendix A for more details):

$$T \cong LE = \frac{\Delta(R_n - G) + \rho C_p g_a (e_{\text{sat}}(T_a) - e_a)}{\Delta + \gamma(1 + \frac{g_a}{g_c(\Psi)})} \quad (1)$$

T is transpiration or latent energy removal by soil and within-leaf evaporation (E), Δ is the slope of the relationship between vapor pressure and air temperature, R_n is net radiation, ρ is air density, C_p is air heat capacity at constant pressure, g_a is aerodynamic conductance, $e_{s(T_a)}$ is the saturated vapor pressure at air temperature; e_a is air vapor pressure; L is the latent heat of vaporization, γ is the psychrometric constant and $g_c(\Psi)$ is canopy conductance that is dependent on plant Ψ and based upon stomatal conductance's of individual leaves. Note that this general formulae is effectively the same as the reference ET_o formula used elsewhere (Allen et al., 1998), but has a unit transformation and lacks the specific constants for a grassy reference surface. The predicted relationship between T and water potential for varying evaporative demand (ET_o) is a decreasing line, where greater evaporative demand results in higher T and more negative Ψ (Fig. 1a). But, variation in soil water deficit results in T decreasing with lower Ψ at constant ET_o (Fig. 1b). The demand and supply responses (Fig. 1a and b) are contrasting, but meet where the soil water potential and ET_o are the same. The supply function does not reach higher stem water potentials than ~ -1 MPa for a constant ET_o (600 W m^{-2}) as the plant has a finite hydraulic conductance resulting in a gradient from the soil to the stem (Fig. 1b). The demand function increases to the point that stomata close considerably due to negative leaf or stem water potentials, but for the high soil water potential modelled the closure happens at unreasonably high ET_o 's ($>800 \text{ W m}^{-2}$; not shown).

The response of T to limited supply of water in the soil is based on the soil-plant-atmosphere continuum (SPAC) and is represented

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