



The pitfalls of water potential for irrigation scheduling

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ABSTRACT

The water potential (Ψ_p), has been widely used as an indicator of plant water status for irrigation management purposes. The simple infrastructure needed for its measurement and its direct relation to basic plant physiological processes, have contributed to the popularity of the methodology. When used for irrigation scheduling, it is commonly assumed that an unavoidable relationship exists between plant transpiration (T), soil water content and Ψ_p . Nevertheless, it is worth remembering that variations in Ψ_p are not solely related to changes in soil water content, but are also an expression of the interaction between the plant and its environment. We used a soil-plant-atmosphere-continuum (SPAC) model to highlight the importance of considering such interactions through a series of *in silico* experiments. Our analysis shows that evaporative demand, the hydraulic architecture of the plant, and the texture and depth of the soil play key roles in the final Ψ_p observed. To establish irrigation programs based on Ψ_p , without considering the environmental and plant factors that influence it, can create the paradox of having a plant that suffers greater water stress even when high irrigation volumes are applied. The conclusions from our *in silico* analysis provide some warnings that should be considered when using Ψ_p to schedule irrigation.

1. Introduction

Water potential (Ψ_p) is probably the most widespread indicator used to monitor the water status of a plant, but what is it exactly? The Ψ_p measures the energy status of the water in a system, referred to as the energy of free and pure water (Campbell, 1985). Expressed another way, it is the amount by which free Gibbs energy changes when water in a system varies while pressure and temperature remain constant (Campbell and Norman, 1998; Jones, 2013). The Ψ_p can be decomposed into pressure, osmotic and gravity potentials, each affecting the Ψ_p in specific ways. The osmotic potential refers to the osmotic pressure generated in a compartment with solutes (like a cell) separated from pure water by a semipermeable membrane. The pressure potential refers to the difference in hydrostatic pressure from a reference and can be positive or negative (tension). Finally, the gravity potential (often overlooked) results from differences in height from the reference level, i.e. to changes in the potential energy (Jones, 2013; Kramer, 1969). For a more in-depth description of Ψ_p and its components, the reader is encouraged to consult Jones (2013) or Kirkham (2004).

The cohesion-tension theory establishes that the difference in water potential between soil and atmosphere is the driving force for transpiration (T) (Tyree and Zimmermann, 2002b). The catenary hypothesis of van den Honert (1948) provides a useful framework to study the relation between transpiration (T), Ψ_p and soil-plant resistances (R) (van den Honert, 1948). If capacitance is not considered, Ψ_p can be expressed as:

$$\Psi_p = T \cdot R - \Psi_{soil} \quad (1)$$

According to Eq. (1), the measured Ψ_p will depend on the plant transpiration (T), on the soil water potential (Ψ_{soil}) and on the obstacles for the movement of water from the soil to the atmosphere through the plant; i.e. on the resistance (R) to water movement. Changes in R are related to variations in the hydraulic architecture of the plant and in the physical properties of the soil (Sperry et al., 1998; Tyree and Zimmermann, 2002a). Low soil temperatures or dry conditions induce changes in root resistance that modify its uptake capacity (Bristow et al., 1984; Garcia-Tejera et al., 2016; Lopez-Bernal et al., 2015; North and Nobel, 1997a). Xylem cavitation during stress reduces the number of conductive vessels and leads to increased trunk resistance (Pockman and

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Sperry, 2000; Venturas et al., 2017). At a macro scale, changes in root or canopy morphology also alter R. Changes in root-to-shoot ratios have been observed in trees (Mokany et al., 2006). For instance, under water stress there is an increase in root-to-shoot ratios. This plastic response alters the water supply (roots) and demand (leaves) relationship, favoring the maintenance of a better plant water status during drought (Hsiao and Xu, 2000).

One problem with Eq. (1) is that T and Ψ_p are not independent. A negative feedback response is well known between stomatal conductance (g_s) and Ψ_p , affecting T (Buckley, 2019; Buckley et al., 2003; Tuzet et al., 2003). Any decline in Ψ_p below a certain threshold -or critical water potential- will induce stomata closure and reduce T. The sensitivity of the stomata to Ψ_p has been used to classify plants as isohydric or anisohydric. However, the way that these two concepts are defined differs among authors. For Tardieu and Simonneau (1998), the relationship between Ψ_{soil} and Ψ_p at midday during drought defines the iso-anisohydric behavior. An isohydric plant will maintain a constant midday leaf water potential regardless of the Ψ_{soil} , whilst in an anisohydric plant Ψ_p will decline with Ψ_{soil} . In contrast, Martínez-Vilalta et al. (2014) propose use of the slope of the relationship between midday Ψ_p and predawn Ψ_p . If the slope is less than 1 the plant will be isohydric and if it is higher than 1 it will be anisohydric (Martínez-Vilalta et al., 2014). Klein (2014) observed that iso-anisohydric behavior represents a gradient rather than two separate hydraulic states. Given the discrepancies in the definitions and the strong effect that environmental factors have on plant water relations, Hochberg et al. (2018) proposed to abandon the iso-anisohydric terminology and to go for a more fundamental framework based on the direct relation between g_s and Ψ_p . In the present paper, we will follow Hochberg et al. (2018) recommendation.

We have spoken about the sensitivity of the stomata to Ψ_p decline, but growth is the first process that is affected when Ψ_p drops (Hsiao, 1973). The different sensitivities of g_s and growth to changes in Ψ_p have been used to establish irrigation programs. In situations where the objective is biomass production, the goal is the maintenance of a high Ψ_p . Keeping a high Ψ_p ensures plant growth and avoids any photosynthesis limitation, maximizing canopy size and radiation interception (Hsiao, 1973; Tardieu et al., 2018). This strategy is typically used in annual crops, where yield is a fraction of the biomass produced (Evans, 1998). In tree crops and vines, however, economic returns are related to both biomass and crop quality (Ferrerres and Soriano, 2007). The induction of slight to moderate stresses at specific phenological stages through deficit irrigation programs, has been shown to be positively related to fruit firmness and sugar concentration (Basile et al., 2011; Girona et al., 2009; Lopez et al., 2012). The maintenance of a slight water stress allows control of excessive growth, favoring an optimal light environment inside the canopy and improving the partitioning of carbohydrates to reproductive structures (Chalmers et al., 1981; Johnson and Handley, 2000; Jones, 2004).

Irrigation programs based on Ψ_p use thresholds to trigger irrigation. Once the threshold is passed, the irrigation system is triggered. Consequently, the Ψ_p needs to be monitored. The most widely used methodology to measure Ψ_p involves the use of a pressure chamber (Scholander et al., 1965). In the pressure chamber technique, a positive pressure is applied to an excised plant section inside a chamber until the liquid content of the sample is forced out. At this point, the applied pressure equals Ψ_p (Boyer, 1995). For irrigation management purposes, the pressure chamber technique is used at different times of the day. If the measurement is performed during the night, when T is negligible, the Ψ_p can be used as a surrogate of Ψ_{soil} (see Eq. (1)). This is called the predawn water potential (Ψ_{pd}) (Boyer, 1995). On a clear day, the minimum Ψ_p is usually achieved at midday. When the noon measurement is performed on sun-exposed leaves, the value obtained is the midday leaf water potential. However, if the leaf is covered with a plastic bag and sealed for enough time, the leaf water potential equilibrates with the water potential of the stem, giving the stem water potential (Ψ_{stem}) (Levin, 2019).

Given all of the above, several questions arise. If R influences the relationship between T and Ψ_p , what are the implications of changes in R through variations in soil texture or plant morphology? How will plants with different Ψ_{crit} behave in the same environment? What are the risks of using a discrete methodology to monitor Ψ_p ? What implications does the use of midday or predawn water potential have for irrigation scheduling? To answer these questions, we used a soil-plant-atmosphere continuum (SPAC) model to perform a series of *in silico* (virtual) experiments. The great advantage of using a model is that one of the variables that influence Ψ_p can be varied while all the others can be held constant. In this way, it is possible to explore the complicated interactions between the several factors that define Ψ_p . Thus, the objective of the present paper is to show how the variables that influence Ψ_p might affect irrigation programs based on the water potential.

2. Materials and methods

The effect of changes in SPAC components on the relationship between T, Ψ_p and the relative soil water content (RSWC) was studied through a series of *in silico* experiments. Simulations were performed using the SPAC model with a multi-compartment solution (García-Tejera et al., 2017b). The model has been previously validated on olive trees at different levels of water stress showing its capacity to accurately simulate T and Ψ_p (García-Tejera et al., 2017a). Briefly, the model simulates T and Ψ_p using the catenary hypothesis (van den Honert, 1948), in which the soil-plant-atmosphere system is viewed as a set of resistances either in parallel or in series. The canopy is discretized into sun/shade leaves (dePury and Farquhar, 1997), while the soil is divided vertically into different layers, and split horizontally into two compartments; the wet compartment (F_{wet}) which will include the area influenced by the localized irrigation system, and the dry compartment (F_{dry}) which represents the rest of the soil. These compartments allow characterization of heterogeneity in root length distribution and soil water content inherent to the use of localized irrigation systems. Regulation of stomatal conductance is simulated using the Tuzet et al. (2003) model which includes the effect of water potential changes on stomatal response. The variability of root resistivity (i.e. resistance to water uptake per unit root surface area) to temperature and soil dryness is modeled on the basis of García-Tejera et al. (2016) and Bristow et al. (1984). Fig. 1 shows a schematic representation of the model.

The leaf water potential in the model is calculated for each leaf class (sun or shaded) as:

$$\Psi_{leaf_sun} = \frac{\sum \sum \frac{\Psi_{soil,j}}{R_{sij}+R_{rij}}}{\sum \sum \frac{1}{R_{sij}+R_{rij}}} - g_{s_sun} 1.6 \frac{VPD}{P_{atm}} 0.018 \left(\frac{\sum \sum \frac{1}{R_{s,j}+R_{r,j}} + R_x}{f_{sun}} \right) LAI_{sun} \quad (2)$$

$$\Psi_{leaf_shade} = \frac{\sum \sum \frac{\Psi_{soil,j}}{R_{sij}+R_{rij}}}{\sum \sum \frac{1}{R_{sij}+R_{rij}}} - g_{s_shade} 1.6 \frac{VPD}{P_{atm}} 0.018 \left(\frac{\sum \sum \frac{1}{R_{s,j}+R_{r,j}} + R_x}{f_{shade}} \right) LAI_{shade} \quad (3)$$

The right-hand term in Eqs. (2) and (3) include the resistances of: the soil (R_s), the root (R_r) and the xylem (R_x), the vapor pressure deficit (VPD), the atmospheric pressure (P_{atm}), the leaf area index (LAI), the fraction of sun and shade leaves in the canopy (f_{sun} , f_{shade}) and the soil water potential at the corresponding soil site ($\Psi_{soil,i,j}$). The subscripts i and j in the resistances correspond to the soil layer and compartment

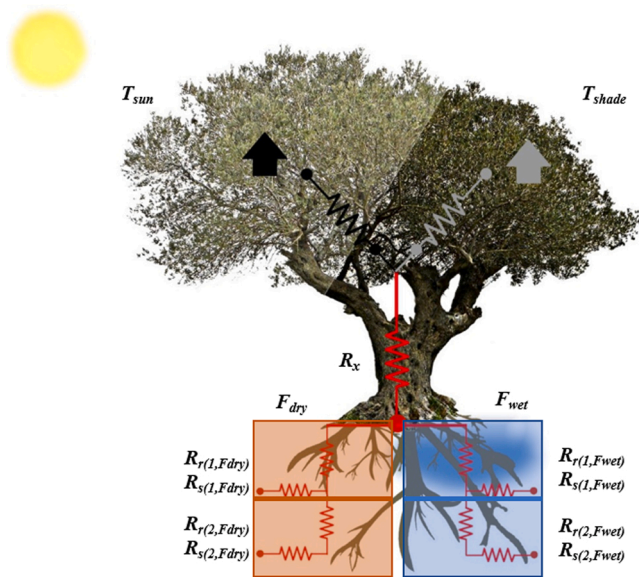


Fig. 1. Schematic representation of the SPAC model with a multi compartment solution. The resistance in red represent the obstacles for the water movement through the soil towards roots rhizosphere (R_s), from root rhizosphere to root xylem (R_r) and from root xylem to shoots (R_x). The black and grey resistances represent the resistance of the stomata for sun and shade leaves classes. Arrows represents the transpiration for each leaf class (T_{sun} , T_{shade}). Blue and brown rectangles show the fractions of soil influenced by the emitter (F_{wet}) and the rest of the soil (F_{dry}) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

number.

The simulations were performed using olive (*Olea europaea*, L) as the model tree. The weather conditions imposed were obtained from a weather station located in Cordoba (37.86 °N 4.80 °W, Spain). Inputs for the model were obtained from the literature except those specifically modified for the *in silico* analysis. The sources of the model parameters are summarized in Supplementary Material 1. The *in silico* experiments were as follows:

2.1. Ground cover variations

Two different ground covers (GC) were compared on a high density (408 trees ha⁻¹) olive orchard: a GC of 40 % (GC40) and a GC of 20 % (GC20). The ground cover was defined as the projected shadow of the tree crown when the sun is at noon.

The simulations explored the effect of a pruning event on the relationship between Ψ_{stem} at noon and RSWC. For each GC, the RSWC was changed from field capacity to permanent wilting point. The same weather conditions were used for all the imposed RSWCs. The canopy parameters (except the GC values) were obtained from [Iniesta et al. \(2009\)](#), whilst root distribution was adapted from [Moriani \(2001\)](#). Parameters used for the two soil textures were obtained from [Campbell and Norman \(1998\)](#). The soil depth was 1.5 m. The rest of the parameters required to run the model were obtained from [García-Tejera et al. \(2017a\)](#). The weather conditions used were those of a clear summer day (DOY 234, the year 2014). Simulations were performed on two soil textures, sandy and clayey.

2.2. Effect of stomata sensitivity to stem water potential changes

Stomatal sensitivity to Ψ_p was varied through modifications of two parameters in the model of [Tuzet et al. \(2003\)](#), namely the water potential that reduce g_s to half (Ψ_{crit}) and the sensitivity of g_s to Ψ_p changes (s_f). The values of the modified parameters are included in [Table 1](#). In the simulations, the relationship between T and Ψ_{stem} was compared on

a clear summer day at different RSWC and for two plants with distinct stomatal conductance sensitivities to the water potential; one of high sensitivity (HS) in which $\Psi_{crit} = -1.2$ MPa and $s_f = 2.3$ MPa⁻¹ and one of low sensitivity (LS) in which $\Psi_{crit} = -2.6$ MPa and $s_f = 4.9$ MPa⁻¹. As in experiment 2.1, the *in silico* analysis was performed changing the RSWC from field capacity to permanent wilting point using the same weather conditions for each value of RSWC. In both treatments the RA:LA = 4.79. The weather conditions were the same as in experiment 2.1. Soil texture parameters were those for a sandy soil ([Campbell and Norman, 1998](#)) and soil depth was 1.5 m.

2.3. Root distribution and pre-dawn water potentials

The changes in Ψ_{PD} due to variations in root distribution and soil water content were analyzed. To do so, the proportion of roots in each soil compartment and soil layer was changed while total root biomass was maintained. The region of soil influenced by the wet bulb (F_{wet}) was changed from field capacity (RSWC = 1) to 0.25 of RSWC while the rest of the soil (F_{dry}) was set at 0.1 of RSWC. Soil conditions were the same as in experiment 2.2, namely, sandy soil of 1.5 m depth. The weather conditions used were those of a spring day (DOY 149).

2.4. Irrigation scheduling using a common stem water potential

Two olive orchards with different tree densities were compared: super high density (SHD, 1666 tree ha⁻¹) and high density (HD, 408 tree ha⁻¹). Data inputs for the SHD were obtained from [García-Tejera et al. \(2017a\)](#). The root-to-leaf area ratio (RA:LA) was different in both orchards, with the HD having a higher RA:LA than the SHD ([Table 1](#)). Irrigation in both SHD and HD was 1.14 mm h⁻¹. Irrigation scheduling was established using a threshold midday $\Psi_{stem} = -2$ MPa in accordance with [Ahumada-Orellana et al. \(2019\)](#). Whenever Ψ_{stem} fell below the threshold during the simulation, irrigation was triggered for 10 h (thus applying 11.4 mm per irrigation event). The simulation period ranged from DOY 127 (May 1st) to DOY 274 (October 1st). At the beginning of the simulation, the soil was assumed to be at field capacity. Soil depth was 1.5 m with a sandy loam texture. Data for the soil characteristics were obtained from [Campbell and Norman \(1998\)](#).

3. Results

3.1. Simulation 2.1. (Different ground covers)

[Fig. 2](#) show the effect of different groundcovers on the relationship between Ψ_{stem} at noon and the RSWC. The GC40 treatment presented a lower Ψ_{stem} for the same RSWC when compared to GC20. However, the magnitude of the differences between the treatments was not the same for the two soil textures considered. In the sandy soil, there was a steeper decline in Ψ_{stem} in GC40 compared with GC20 as the RSWC was reduced. In the clayey soil the difference throughout the RSWC range was maintained in both treatments, but GC20 always presented a higher Ψ_{stem} . The root area for both treatments was the same. The larger RA:LA ([Table 1](#)) in GC20 was the consequence of a reduction in leaf area.

3.2. Simulation 2.2. (Stomatal sensitivity to Ψ_p)

The response of two stomatal behaviors under water stress is presented in [Fig. 3](#). Each point represents the T- Ψ_{stem} relationship for an RSWC value. The HS plant presented a lower T at the initial point when the soil was at field capacity. The transpiration demand imposed during this experiment was high, with a reference evapotranspiration of around 6 mm day⁻¹ and a temperature at noon of over 30 °C. Under such weather conditions, even for a soil entirely at field capacity, the water potential drop was enough to affect stomatal conductance in the HS. Therefore, T was reduced with respect to the LS. The higher g_s sensitivity of the HS also influenced the initial Ψ_{stem} . In the LS plant, at field

Table 1

Summary of soil conditions, evaporative demand, stomata sensitivity to water potential and root-to-leaf area ratios (RA:LA) applied to the four *in silico* experiments. GC20 and GC40 represent the treatments with 20 % and 40 % of ground cover. HD and SHD are the high (408 tree ha⁻¹) and super high density (1666 tree ha⁻¹) orchards. HS and LS are high and low sensitivity of the stomata to variations in Ψ_p .

	Exp. 2.1		Exp. 2.2		Exp. 2.3	Exp. 2.4	
	GC20	GC40	HS	LS	HD	HD	SHD
Soil Texture	Sandy & Clayey	Sandy & Clayey	Sandy	Sandy	Sandy	Sandy Loam	Sandy Loam
Evaporative Demand	High	High	High	High	Low	High	High
RA:LA	13.55	4.79	4.79	4.79	4.79	4.79	3.0
Ψ_{crit} (MPa)	-1.0	-1.0	-1.2	-2.6	-1.0	-1.0	-1.0
s_f (MPa ⁻¹)	2.3	2.3	4.9	2.3	2.3	2.3	2.3

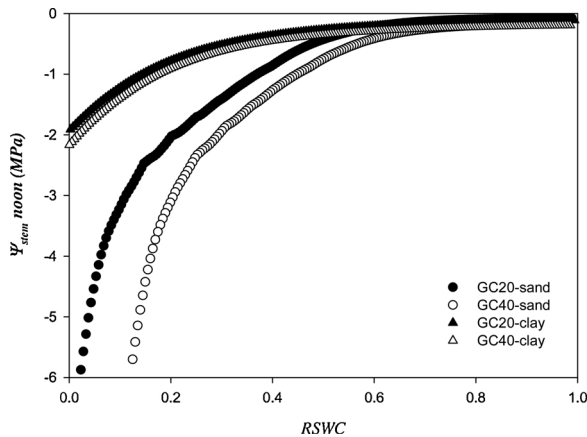


Fig. 2. Effect of ground cover (GC) on the relation between the relative soil water content (RSWC) and the stem water potential at noon (Ψ_{stem}) in a sandy and clayey soil texture.

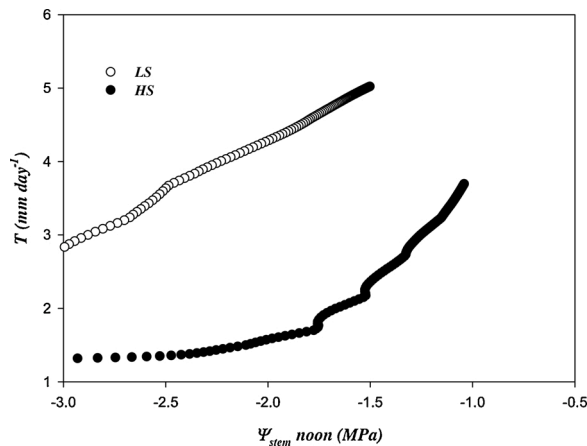


Fig. 3. The relation between transpiration (T) and stem water potential at noon (Ψ_{stem}) at high (black dots, HS) or low (white dots, LS) critical water potential (Ψ_{crit}). Each point corresponds to a soil water content applied to the entire soil profile.

capacity, the Ψ_{stem} was -1.5 MPa whilst in the HS, it was -1 MPa.

During the simulation, the two plants had different T but the T- Ψ_{stem} relation was linear. However, at a Ψ_{stem} below -2.5 MPa T remained constant in the HS treatment. In this treatment, when $\Psi_{stem} = -2.5$ MPa, g_s reached its minimum value. At this point any further decline in the RSWC and hence Ψ_{stem} did not modify g_s with T remaining constant.

3.3. Simulation 2.3. (Variation in predawn water potential)

Fig. 4 shows how the water available in the soil and the root

distribution profiles affected Ψ_{PD} . The RSWC in the alley was set to 0.1 in all the simulations, mimicking a dry situation. The changes in water content were applied only to the wet compartment (F_{wet}). As the soil dried, the Ψ_{PD} went down. Ψ_{PD} passed from -0.03 MPa when the RSWC in $F_{wet} = 1$ to -0.6 MPa when the RSWC in $F_{wet} = 0.25$ at the maximum fraction of roots. The variations in Ψ_{PD} due to changes in the root distribution became significant when RSWC = 0.25. When the RSWC in F_{wet} was at 0.25 the difference between the highest and the lowest root fraction was -0.2 MPa.

3.4. Simulation 2.4. Irrigation scheduling with a common Ψ_{stem}

The simulated Ψ_{stem} at noon is shown in Fig. 5. During June, July and August (DOY 152 to 243) deviations of the simulated Ψ_{stem} from the threshold (dashed line in Fig. 5) were observed. The minimum Ψ_{stem} during the simulation period was -2.6 MPa in HD and, -3.6 MPa in SHD. The number of times for the thresholds being exceeded was greater in SHD than in HD. Consequently, the cumulative Ψ_{stem} below the threshold was -50.5 MPa in the SHD, whereas for the HD was -26.7 MPa.

Fig. 6 shows the cumulative irrigation in the HD and SHD treatments. Despite the higher cumulative Ψ_{stem} for SHD, the total amount of water applied in this orchard was greater than in the HD, with respective values of 216 mm and 148 mm (Fig. 6). This difference was only due to a higher number of irrigation events in SHD, since the volume of water applied in each irrigation event was the same in both treatments. Although the Ψ_{stem} threshold was set to avoid plant stress, significant differences in T with respect to a well-watered tree were observed (Fig. 7). Fig. 7 shows the cumulative difference in T between the simulations presented in section 2.4 and the same tree with the soil always

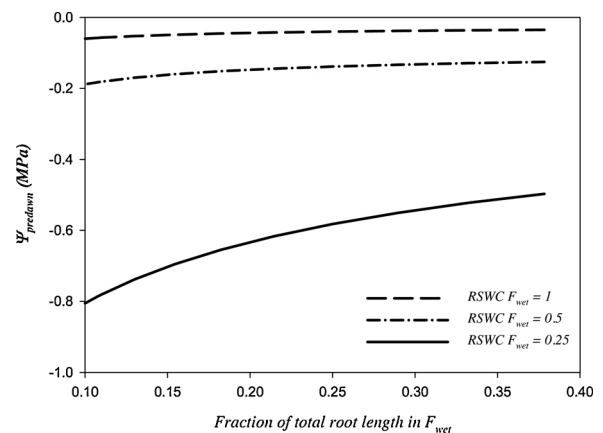


Fig. 4. Predawn water potential variations at different root distributions. Each line represents a relative soil water content value (RSWC) in the wet compartment (F_{wet} , see Section 2 for a definition of the wet compartment). Global root biomass was kept the same for all the simulations, and the only thing that was changed was the amount of root in each soil layer and compartment. The RSWC in the alley was 0.1 in all the simulations.

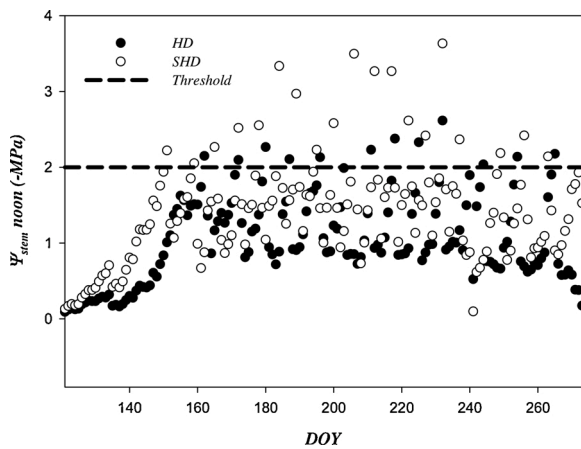


Fig. 5. Stem water potential at noon (Ψ_{stem}) during the simulation period for the high density (HD) and the super high density (SHD) orchards. The dashed line indicates the threshold to trigger irrigation, which was established at Ψ_{stem} of -2 MPa at solar noon.

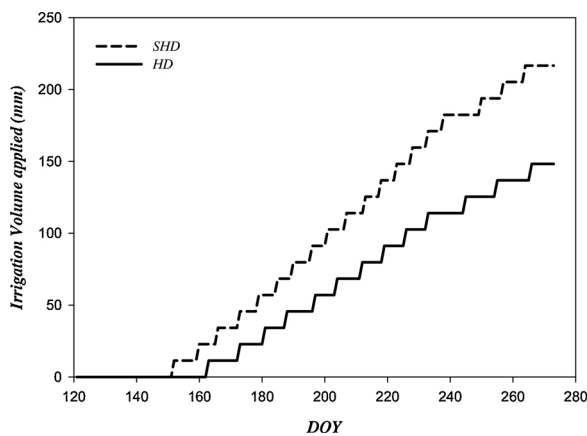


Fig. 6. Cumulative irrigation in SHD (dashed) and HD (straight).

at field capacity, i.e. at its potential T . It can be seen how; the trees were under water stress in both cases. However, the SHD presented a greater difference, with a minimum value of -370 mm compared with the -247 mm in HD. These results are in accordance with the larger deviations

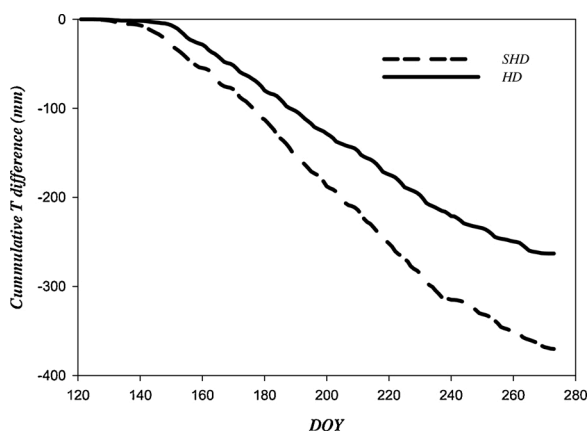


Fig. 7. Cumulative transpiration (T) difference in SHD (dashed line) and HD (continuous line). Values were calculated as the cumulative difference between transpiration obtained when a -2 MPa Ψ_{stem} threshold was used to trigger irrigation and the transpiration obtained when the soil was kept at field capacity during the entire simulation period.

from the Ψ_{stem} threshold observed in Fig. 5 for SHD.

4. Discussion

4.1. Effect of variation on the resistances (R)

The R is the result of the soil and plant characteristics (Campbell, 1985). It is the sum of several resistances that form the water path from the soil to the atmosphere through the plant: the soil resistance, which includes the water movement from the midpoint between two roots towards the rhizosphere (Gardner, 1960); the radial root resistance, which represents the radial movement of water from the rhizosphere towards the xylem in a composite transport – meaning that water can move through apoplastic or symplastic pathways (Steudle and Peterson, 1998); and the xylem resistance which is defined by the tree hydraulic architecture (Pockman and Sperry, 2000; Tyree and Ewers, 1991). The importance that each of them plays on R depends on the environmental and plant conditions (Sperry et al., 1998; Tyree and Zimmermann, 2002c).

During periods of drought, the RA:LA and the soil texture will regulate whether the limiting path for water transport will be the xylem or the roots (Sperry et al., 1998, 2002). The model does not simulate changes in xylem resistance by cavitation, but it does include variations in root (including the rhizosphere) resistance during drought using the approach of Bristow et al. (1984). The effect of cavitation on Ψ_p has recently been questioned by Dietrich et al. (2018) who showed how a reduction of more than half of the xylem area did not affect Ψ_p . The absence of a cavitation effect on xylem resistance explains why there is a steep drop in Ψ_{stem} for the sandy soil, whilst in the clayey texture the Ψ_{stem} is maintained until the RSWC equals zero (Fig. 2). For coarser textured soils and low RA:LA, the roots are the bottle-neck for water transport during drought. As the soil texture becomes finer or the RA:LA increases, the role of the xylem in transporting water becomes more important (Sperry et al., 1998). These shifts in the main element that limits water transport can have implications beyond irrigation scheduling. A breeding program whose main aim is to improve tree water status through more profuse root systems will have little advantage in areas with clayey soils.

In Eq. (1) we showed that R and T affect Ψ_p , and so changing R will necessarily alter Ψ_p (Fig. 2). For instance, when we prune a tree we reduce the RA:LA, modifying the plant's hydraulic architecture. The result is an improvement of the plant water status (higher Ψ_p) for the same weather and soil conditions (Li et al., 2003). In fact, trees tend to naturally modify R through changes in its hydraulic architecture. The Huber value (mm^2 xylem cross-section g^{-1} leaves fresh weight) varies among species and in branches of the same tree. It is known that plants from dry environments have higher Huber values than those from more humid ones. Even in the same tree, lateral branches will be in worse hydraulic conditions than apical ones, due to lower Huber values (Tyree and Zimmermann, 2002c). This variability in Huber values within individuals tends to compensate for the larger paths on distal branches allowing them to be in better hydraulic conditions than laterals (Tyree and Ewers, 1991). The result is a more uniform Ψ_p distribution throughout the tree. Root morphology plays a role too in tree Ψ_p distribution. Tap or herringbone shapes induce significant differences in Ψ_p throughout the root system and hence the plant (Doussan et al., 1998; Javaux et al., 2013); with the magnitude of such differences mediated by the soil texture (Javaux et al., 2008). Even changes in root distributions associated with the presence of wet spots modify the final Ψ_p observed (Ameglio et al., 1999). Hence, Ψ_p is not just a consequence of the soil water content or the evaporative demand, but is also an expression of the interaction between the plant, the soil and the environment.

4.2. Changes in Ψ_{crit}

The Ψ_p has been used to estimate T in plants that present a linear

relation between the water potential and the transpiration (Choné, 2001; Garnier et al., 1988; Williams et al., 2012). Simulation 2.2 shows that a linear relationship between Ψ_p and T exists, but the slope of this relation is dependent on Ψ_{crit} (Fig. 3). Differences in Ψ_{crit} are quite common, especially in *Vitis vinifera* L. (Levin et al., 2019). The fact that the relationship between Ψ_p and T is linear implies that R is independent on Ψ_p and T. However, it was seen in simulation 2.1, that R changed when we modified the soil and the plant characteristics. Schultz (2003), observed how, the slope of the linear relationship between T and leaf water potential differed between two grapevine cultivars due to their distinct plant sizes. If the slope results from R and Ψ_{crit} , there will be as many T- Ψ_p relations as possible R and Ψ_{crit} combinations. Thus, the T- Ψ_p relation will be site specific and any extrapolation could lead to significant errors in the estimation of T using Ψ_p .

The use of a common threshold to schedule irrigation in plants with different Ψ_{crit} can trigger irrigation even when the soil is at field capacity. Fig. 3 shows how the midday Ψ_{stem} on a clear day is lower for the HS than for the LS plant at maximum T. If we set the irrigation threshold to avoid any stress based on HS water potential at field capacity, we will trigger irrigation on LS even when there is enough water in the soil.

4.3. Predawn water potential as an indicator

The predawn water potential (Ψ_{PD}) is commonly used as a surrogate for the soil water potential (Richter, 1997; Ritchie and Hinckley, 1975). At night, when the stomata are closed and T is negligible, Ψ_{soil} is balanced with Ψ_p (Kramer, 1969). During the equilibrium process between Ψ_{soil} and Ψ_p , the roots connect the soil and the plant, and the Ψ_{PD} becomes an estimation of the portion of the soil perceived by the roots (Ameglio et al., 1999). It is important to keep in mind the “perceived by the root system” part of the preceding sentence. Roots are unevenly distributed throughout the soil (Huang and Eissenstat, 2000; Jackson et al., 1996), especially under localized irrigation (Clothier and Green, 1997; Klepper, 1991). Ameglio et al. (1999) in an experiment with walnut (*Juglans regia* L.), demonstrated that Ψ_{PD} is indeed a surrogate of Ψ_{soil} but weighted by the resistances of the roots and the soil. Fig. 4 supports the work of Ameglio et al. (1999). The effect of the resistances is clear when a reduction of RSWC in F_{wet} produces a concomitant decline in Ψ_{PD} for the same root distribution. In the simulation, the root resistance increased as we reduced the RSWC in F_{wet} . This process also happens in the field. The root system gradually increase its resistance during drought, either through suberification of the exodermis or by loose contact between the root surface and the soil particles (North and Nobel, 1992, 1997a; North and Nobel, 1997b). The result is a decoupling of the roots from the soil in the driest areas (Gardner, 1960; Javaux et al., 2008; Sperry et al., 1998). Therefore, the Ψ_{PD} observed will represent the Ψ_{soil} of the wettest region (the wet bulb in a drip irrigation system) and not an average of the entire soil.

The practical consequences of using Ψ_{PD} are not trivial. Fig. 4 show how just a 10 % of the root system, is responsible for the high Ψ_{PD} observed when the RSWC in the wet bulb is as low as 50 % of field capacity. Therefore, when the wetted volume of soil becomes very small, the ability to sustain transpiration during the day will be compromised, even when Ψ_{PD} values are close to field capacity. The small fraction of wetted roots will be unable to provide enough water to satisfy the canopy demand.

Finally, it is important to bear in mind that the use of Ψ_{PD} as a surrogate for soil water potential relies on the assumption of an equilibrium between plant and soil. Such equilibrium cannot be reached when the nights are either too short (summer in northern latitudes) or under weather conditions that induce significant nighttime transpiration rates (Richter, 1997).

4.4. Practical implications of a common threshold

The effect of using a common Ψ_p threshold to schedule irrigation is

shown in Figs. 5–7. Despite having the same Ψ_{crit} , soil characteristics and weather conditions, setting a common Ψ_p led to very different plant responses between the HD and SHD orchards. In experiment 2.4, we checked Ψ_{stem} exactly at noon. If Ψ_{stem} values below the threshold happened later in the afternoon the irrigation was not triggered. Although this situation was common for both treatments, it induced larger deviation from the thresholds in SHD (Fig. 5). In Section 4.1 we discussed the effect of a changing R on Ψ_p . Fig. 2 showed that a reduced RA:LA will induce a steeper decay in Ψ_{stem} as the soil dries, particularly for coarser soil textures. The SHD had an RA:LA ratio 40 % lower than the HD, and the soil texture used for the simulations was a sandy loam (Table 1). Hence, the negative effect of not triggering irrigation was exacerbated in SHD (Fig. 5). Moriana et al. (2012) observed how setting a common irrigation threshold produced a higher water stress integral (MPa-day) in trees with larger GC fractions, especially in the deficit irrigation program in which the threshold was set at -2 MPa where the authors found that the treatments with a higher GC presented a larger reduction in growth and yield (Moriana et al., 2012). The results obtained by Moriana et al. (2012) contrast with the conclusions of Ahumada-Orellana et al. (2019) who observed that a $\Psi_{stem} = -2$ MPa will keep trees at mild or no stress. The differences found between the two studies exemplify the level of specificity of irrigation thresholds.

We have assumed that Ψ_{stem} measurement was discrete, like those obtained with a pressure chamber. Nevertheless, continuous Ψ_{stem} recording is possible. Stem psychrometers or the leaf pressure clamp allow for high frequency Ψ_{stem} records (Coffey et al., 1997; Quick et al., 2018; Zimmermann et al., 2008). The use of continuous Ψ_{stem} recording will reduce the differences observed in Fig. 5, if the irrigation is triggered immediately after the Ψ_{stem} threshold is surpassed. However, farms commonly have different irrigation blocks and water is delivered in irrigation water turns, meaning that a lag will exist between the signal from the sensor and the system’s availability to deliver water to the plant. If the time elapsed between the triggering signal and the irrigation event is too long, there will be no advantage in the use of a continuous system.

In the simulation, the irrigation amount was not related to the soil water content. This explains the higher number of irrigation events in SHD (Fig. 6). If the irrigation volume did not recover Ψ_{stem} to a value below the threshold, irrigation was triggered again the next day applying the same amount of water. Consequently, despite the higher water use in SHD, the cumulative T was lower (Figs. 6 and 7). The Ψ_{stem} indicates when to trigger irrigation but not how much is needed (Jones, 2004). To schedule irrigation, Ψ_p needs to be monitored together with the soil water content to know when to irrigate and how much water is required.

5. Conclusions

The Ψ_p has been widely used to schedule irrigation. However, it is important to bear in mind that the Ψ_p observed in a plant is not only a function of the available water in the soil but is also an expression of the interactions of all the elements that conform the SPAC. Therefore, the use of absolute thresholds to provide irrigation advice could induce significant errors in situations where the conditions are very different from the ones in which the Ψ_p references were established. The interpretation of Ψ_p should be carried out inside the SPAC framework, otherwise, misleading conclusions might arise from interpreting the data solely based on the interaction between Ψ_p and the water stress level. In this regard, the use of models like the one applied for the *in silico* experiments in this paper will help to separate the wheat from the chaff.

In summary

- The Ψ_p responds not only to water shortage but also to other factors including cultivar, environment, soil type and the relationships between canopy and root system, i.e. the resistances to water

movement (R). Hence the water potential thresholds to schedule irrigation are site-specific.

- Any natural or anthropogenic modification of the RA:LA will induce changes in the relationship between T, Ψ_p and soil water content. The same is true for plants with different Ψ_{crit} .
- The Ψ_{pd} is not a surrogate of the soil water potential, but an integration of the soil explored and “perceived” by the entire root system, i.e. it is an average Ψ_{soil} weighted by the resistances of the roots and the soil throughout the entire soil profile. The soil water content and distribution, the root area and its conductivity will determine the observed Ψ_{pd} .
- To schedule irrigation, both Ψ_p and the soil water content must be monitored to know when to trigger irrigation and how much water is needed.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agwat.2020.106522>.

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