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Article

Plant Water Status Indicators for Irrigation Scheduling Associated with Iso- and Anisohydric Behavior: Vine and Plum Trees

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Abstract: Plant water status indicators have been increasingly used for scheduling irrigation. Different variables may be used to do this, depending on personal preferences and the resources available. Many studies have suggested that selection of an indicator should take into account plant behavior in relation to isohydricity. In two Iberian studies, deficit irrigation (DI) was applied in a vineyard and in a plum orchard while plant water status and fluxes were monitored. These case-studies are discussed with special focus on the use of predawn leaf water potential (Ψ_{pd}) versus stem water potential (Ψ_{st}) to determine whether Ψ_{st} performed better and would therefore be the preferred stress indicator for plants exhibiting anisohydric behavior. In contrast, in plants with isohydric behavior, Ψ_{pd} would be generally preferred. This hypothesis seems to be supported by the present results obtained and by prior studies. The cultivars used and the intensity of stress applied have an important influence on the results. This suggests that, if no specific information is available from the existing literature, daily preliminary studies would be recommended prior to application in order to select the most appropriate plant water stress indicators.

Keywords: water management; water stress; deficit irrigation; leaf potential; stem diameter; transpiration; orchards; drought tolerance; drought avoidance

1. Introduction

Scheduling deficit irrigation (DI) in commercial fields traditionally requires knowledge of stress coefficient functions (Ks) in order to estimate soil water depletion (SWD) via the water balance, using estimated actual evapotranspiration (ETa) as input. This enables users to anticipate the required irrigation depths (how much water to apply). The use of water stress indicators to schedule irrigation requires the selection of which variables should be used as well as their threshold values for different objectives concerning marketable yields (when to irrigate). Finally, the coordinated use of these approaches or steps can lead to a self-learning process, as proposed by Ferreira [1]. The use of soil water content (θ_s) can directly serve both purposes (when and how much), and is considered the ideal variable in low continuous crops though it presents several challenging difficulties when applied to woody crops. Application to woody crops is especially critical when plants present a significantly active part of their root systems in deep layers, as in agroecosystems found in regions with Mediterranean type climates. Under such conditions, plant water status has often been preferred.

The use of plant water status to schedule irrigation has been advocated since the 1980s by many researchers [2,3] and has seen a continuous rise in its use [4–6]. A risk of using this approach in DI is that water status needs to be accurately maintained within a fairly narrow range as described by Jones [7]. Any excess application loses the benefit of the regulated deficit applied and any sub-application can lead to severe losses in yield or quality. Indeed, if water stress indicators, such as those based on plant water status, are used without estimating SWD, the exact amounts of water to be applied must be calculated from various tests that may result in an excessive or deficient amount of irrigation water, until the desired amount is found (trial and error [1,8]).

In both situations mentioned above, i.e., either estimating SWD or not, plant water status [see 8] is often quantified by using leaf water potential (Ψ_l), generally at predawn (Ψ_{pd}), or stem water potential, measured generally around or shortly after solar noon (Ψ_{st}). A common alternative is the use of stem diameter variations (SDV) and derived indexes. These last indexes are calculated based on easy, affordable and automatable measurements made with linear variable displacement transducers (LVDT, e.g., [9–13]).

The values of Ks have been related to either soil or plant water status. The variables generally used include (i) SWD [14,15], usually expressed in total depth (mm) or (ii) plant water potential (Ψ_{pd} or Ψ_{st}) [16,17]. Though numerous studies have used SDV, results relating Ks with SDV-derived indexes are unfortunately not frequent or have not been successful.

Plant water status does not depend solely on atmospheric conditions and the availability of water in the soil, in general. Plants are able to modify the architecture of their canopies to acclimate to the environment [18] and have several strategies to deal with it including the avoidance of excessive losses by dehydration [19]. In this sense, lowering stomatal conductance (gs) is one of the most effective mechanisms [20–22].

Plants that preferentially put into action effective mechanisms to regulate their water content have a behavior known as isohydric [23,24], whereas those in which the mechanisms referred to above are less effective or non-existent are called anisohydric.

Several studies based mainly on forest species have considered two categories in which species can be classified (e.g., related to xylem type). In this paper, we prefer to use the word “behavior”, which can be ‘more’ or ‘less’ isohydric, or speak about levels of isohydricity. Indeed, many cases have been observed with cultivars displaying different behaviors, notably with grapevines (*Vitis vinfera* L.) [18,25], or even different behaviors for the same cultivar depending on environmental conditions [26–28] or crop stage [29].

Physiological mechanisms associated with isohydricity have been analyzed, as well as their consequences for SDV and plant water potential or the role of stomatal closure. Simonneau et al. [30], when studying SDV in different organs in relation to the water storage rate in 3- to 5-year-old peach (*Prunus persica*) trees, showed that SDV is closely related to total water stored in the shoots, without any important lag. In spite of changes in the volume of water stored (capacitance), which are more or less proportional to the changes in organ volume depending on tissue elasticity [31,32], the changes in plant organ capacitance have been related to SDV, either in the trunk or in branches.

It might be expected that organs from plants with less effective stomatal closure would tend to exhibit anisohydric behavior and change their volume more expressively than plants under conditions of isohydric behavior. However, according to Meinzer et al. [33], such an analysis requires consideration of the effect of using stored water (plant capacitance) in preventing decreases in Ψ_l.

Meinzer et al. [34] found contrasting behaviors of *Juniperus monosperma* and *Passiflora edulis* which reflect differences in their capacity for homeostatic regulation of turgor that could represent aniso- and isohydric behavior. Furthermore, Meinzer et al. [35] evaluated metrics of stomatal regulation of Ψ_l during soil drying in eight woody species and assessed whether easily determined leaf pressure—volume traits could serve as proxies for their degree of iso- vs. anisohydric behaviour. According to Garcia-Forner et al. [36], and contrary to their expectations, both of these species (*J. monosperma* and *P. edulis*) exhibited similar stomatal temporal dynamics in response to drought, with little embolism in *J. monosperma* due to its conservative stomatal regulation. This contributed to refuting the concept that very low water potentials during drought are associated with loose stomatal control and with the hypothesis that anisohydric species are more prone to hydraulic failure than isohydric species.

In a review on the relationship between stomatal behaviour, water potential regulation and hydraulic transport, in relation to isohydric and anisohydric classification, Martínez-Vilalta and Garcia-Forner [37] also observed that a tight regulation of Ψ_l (isohydric) is not necessarily associated with greater stomatal control during drought. A continuous range of stomatal sensitivities to water stress in grapevines, closely linked with rootstock, was observed by Lavoie-Lamoreaux et al. [38]. They found that isohydric and anisohydric behavior defined in terms of Ψ_l regulation cannot be used as an indicator of a specific mechanism of drought-induced mortality or as a proxy for overall plant vulnerability to drought.

In spite of the controversy on the importance of stomatal control in this regard, or even the controversy as to which type of behavior corresponds to less drought vulnerability, the analysis by McDowell et al. [39] supports a connection between isohydric behaviour and tighter stomatal control. In addition, their analysis reinforces the hypothesis that the so-called "isohydric species are more likely to die of carbon starvation than hydraulic failure, and that partitioning of mortality between isohydric and anisohydric plants is a function of drought intensity and duration" [39].

Martínez-Vilalta et al. [40] showed that the response of the plant's water potential gradient to declining θs (meaning here soil water availability) is not determined directly by stomatal sensitivity to drought but by the ratio between this sensitivity and the vulnerability of the plant hydraulic system. In their view and words, a plant with highly sensitive stomata closing at relatively high water potentials (less negative) could still show a strict anisohydric behavior, provided its hydraulic system is even more sensitive than its stomata to declining water availability. The same authors also provided a quantitative framework for interpretation of the coordination between stomatal regulation and plant hydraulics in terms of an analysis of isohydricity. Roman et al. [41] described a continuum of isohydric to anisohydric regulation of leaf water potential and Klein [42] also argued that species-specific curves form a continuum, rather than a dichotomy, between isohydric and anisohydric behavior, and suggested the use of water potential at 50% of the maximum gs (Ψ_{gs50}) for a quantitative comparison between species.

In the context of irrigation science, given the sometimes limited information directly available on such vulnerabilities and given the restricted aim of identifying critical variables and their thresholds, we hypothesized that the daily or seasonal courses of Ψ_{pd} or Ψ_{st} in plants under different conditions, together with the relative degree of stomatal closure, can give hints about the behavior of the species or cultivar under given circumstances.

When gs is not measured, the transpiration rate (Tr) may often be available, due to possible automated monitoring. Reductions in Tr could then be used as proxies of gs reductions, even if they are not strictly proportional, due to possible differences in the driving forces. In this context, the daily or seasonal course of Ψ_{pd} or Ψ_{st} in plants submitted to stress compared to well-watered controls is often a good indication of whether plant behavior is isohydric or anisohydric

This article has the following aims: (1) to identify these two behaviors (isohydric and anisohydric), providing examples that explore relationships between the selected variables and Ks (or relative transpiration, RTr) using two case studies; (2) to use the discussion to verify whether the frequent choice made by researchers of plant stress indicators to express water status is related to the isohydric or anisohydric behavior of plants; and (3) to check whether the usual choice of SDV-derived indexes is related with isohydricity.

We hypothesized that, from this analysis, the arguments for possible orientation in the selection of water stress indicators will be reinforced. The examples shown also serve to explain the criteria used in this study to distinguish between the two behaviors.

2. Materials and Methods

2.1. Experimental Sites, Meteorological Conditions and Crop Characteristics

2.1.1. Experiment 1

Experiment 1 was conducted in a commercial drip-irrigated vineyard, planted with the grape (*Vitis vinifera* L.) 'Tempranillo', grafted on 1103P rootstock, with an area of 6.0 ha ("Herdade de Monte Novo e Figueirinha"), at 38.04972 N, 7.9208 W, 200 m above sea level (a. s. l.), located in the Alentejo region near the city of Beja, the warmest and driest region of Portugal (annual 30-year average for precipitation is 572 mm, 5% of which falls during summer; the climate is temperate of Mediterranean type Csa (http://www.ipma.pt/pt/oclima/normais.clima/1971-2000/002/). The grapevines were planted in 2002 (2350 vines ha^{-1}, row orientation ~N-S). The training system was vertical shoot positioning. The vines were spur pruned on a bilateral Royat cordon with 16 buds per vine. There was tillage between the rows and no tillage beneath the canopy. The soil type was a shallow clay vertisol with abundant gravel and few stones. Available water capacity in the soil was low. The soil depth was about 0.6 m, but only a very few fine roots could have explored rock fissures down to a depth of 1.5 m. The leaf area index (LAI) measured at veraison was 2.15, and ground cover was 42%. The meteorological conditions for the location and years of Experiment 1 are summarized in Table 1.

Table 1. Meteorological conditions for the studied years in Experiment 1 and 2; data represent the year averages.

	Year	P (mm)	$T_{average}$ (°C)	HR_{max} (%)	HR_{min} (%)	ETo (mm)
Experiment 1 Beja (Portugal)	2009	418.0	17.66	93.33	40.53	1311.50
	2010	734.6	17.08	94.01	45.44	1222.99
Experiment 2 Vegas Bajas (Spain)	2010	738.7	16.31	88.04	40.56	1317.70
	2014	506.7	16.33	95.74	42.72	1230.79
	2015	328.0	16.45	93.03	38.65	1310.50
	2016	546.0	16.35	99.25	42.96	1236.98

2.1.2. Experiment 2

Experiment 2 was carried out in an experimental orchard located at Finca La Orden (Cicytex), in the "Vegas Bajas" area (Badajoz, Spain) at 38.8507 N, 6.6709 W, 184 m a.s.l. The soil type is an alfisol characterized as a young soil with low organic matter and a texture of 19.4% clay, 40.2% silt and 40.4% sand. The climate is temperate of Mediterranean type with Atlantic influence (Csa); annual evapotranspirative demand is 1295 mm, with 428 mm annual rainfall. The plant material was *Prunus salicina* 'Angeleno', a late season plum variety grafted on Marianna pattern 2624 rootstock. The orchard was established during 2005, and the tree formation system is in open-beaker with four branches per tree. The arrangement of the trees was in rows in a 6 × 4 m plantation frame, east-west oriented. The meteorological conditions for the location and years of Experiment 2 are summarized in Table 1.

These two Experiments (1 grapevine, 2 plum orchard) were selected for their respective representation of isohydric and anisohydric behavior.

2.2. Measurements and Irrigation Treatments

2.2.1. Experiment 1

Irrigation treatments. The experimental work reported took place during 2009 and 2010. Irrigation started when vegetative growth stopped and was usually applied once a week, on average.

DI treatments were imposed after day of the year (DOY) 175 (approximately two weeks before veraison) until harvest (DOY 238).

During 2009, three DI treatments with three completely randomized repetitions each were applied in the long term. Threshold values of Ψ_{pd} defined for the vineyard [43,44] were used to control stress levels corresponding to irrigation depths applied of approximately 70%, 40% and 25% of estimated crop evapotranspiration (ETc). The aim was for the treatments to correspond in the long term roughly to weak ($\Psi_{pd} > -0.4$ MPa), mild (-0.4 MPa $< \Psi_{pd} > -0.6$ MPa) and severe water stress ($\Psi_{pd} < -0.6$ MPa).

In the following year (August 2010), a short water stress cycle (eight days) was conducted for a more detailed characterization of Ψ_l and stomatal conductance behavior between irrigation events. A control (without water stress (CT)), mild water stress (MS) and moderate water stress (HS) treatments were imposed under field conditions, as follows. Before the beginning of the drought stress (8th August), an irrigation event of 22 mm was applied to CT and MS and of 14 mm to HS. During the water stress period, two irrigation events of 13 mm each were applied to CT (11th and 13th August). Measurements of Ψ_{pd} were taken at predawn, and of Ψ_{st} and gs in the middle of the morning (10 h), 15 min after solar noon (14 h) and at mid-afternoon (18 h).

Measurements. For the long-term experiment of 2009, meteorological data from a nearby station (http://www.cotr.pt/ema.asp?id=1007, 38. 0375 N, 7.8850 W, ca. 206 m a.s.l.) were used to calculate ETo with the Penman-Monteith equation, using reference crop parameters (grass with a height of 0.12 m, surface resistance of 70 s m^{-1} and albedo of 0.23 [15]. ETc was initially established with the crop coefficient as a function of leaf area index (LAI).

All measurements of Ψ_{pd} and Ψ_{st} were performed the day immediately before irrigation with a pressure chamber (Scholander type, PMS Instrument Company, Albany, OR, USA, Model 600) with each leaf for Ψ_{st} wrapped in an aluminum bag two hours prior to measurements. The leaves were removed from the vines and measured in a pressure chamber with the precautions described by Shackel et al. [45]. Stomatal conductance was measured with a LI-1600 steady state porometer (LI-COR Inc., Lincoln, NE, USA). At least three measurements were performed per replicate (9 per irrigation treatment). Due to the soil nature (gravel), θ_s was not measurable.

2.2.2. Experiment 2

Irrigation treatments. For the first part of the experiment, in 2010, two irrigation treatments were established: a Control treatment (C) which was irrigated with 100% of estimated ETc and a Deficit Irrigation (DI) treatment irrigated as C, except from the 7th of June to the 26th of July (48 days) during which there was no irrigation at all (functioning as a stress cycle). The experimental design was four random blocks per treatment, four trees per block. During three consecutive years (2014, 2015, 2016), the same irrigation treatments were maintained. The periods in which irrigation was removed in the stressed (DI) treatment were from 12th May to 11th June in 2014 (30 days), 13th May to 15th June in 2015 (32 days) and 13th May to 22nd June in 2016 (40 days).

Measurements. In 2010, ETc was estimated as the product of ETo obtained with the Penman-Monteith equation and a single Kc according to the values proposed in Allen et al. [15]. In 2014, 2015 and 2016, a soil water balance was used to determine ETc (for C or equivalent). It (ETc $_{WB}$) was calculated using the law of mass conservation (water balance) as:

$$\mathrm{ETc}_{\,WB} = P + I - D - R - \Delta S \tag{1}$$

$$\Delta S = \Sigma\,(\theta_i - \theta_{i-1})\,z \tag{2}$$

where P is effective rainfall, I is irrigation, D is drainage, R is runoff, ΔS is the change in soil water storage between two consecutive dates, and z is the depth of each layer. The values of R were considered negligible because the orchard was levelled and no runoff was observed. D was considered null at the maximum observed depth (1.8 m). The values of θ_s were obtained from neutron probe measurements (CPN 503DR Hydroprobe, CPN International, Inc., Port Chicago Highway, CA, USA), carried out once a week, early in the morning, throughout the irrigation season in the root zone of representative trees of each cultivar. Four access tubes were installed on both sides of a tree at 0.5 m and 1.5 m in a line and, perpendicularly, at 0.5 m and 1.5 m from that line, respectively. Each tube was 3 m long, and measurements were made at intervals of 30 cm, from 30 to 270 cm. The neutron probe readings were calibrated in loco.

In 2010, four times during the season, Ψ_{st} was measured from predawn to sunset at different hours. The measurements were taken for eight trees per treatment corresponding to four trees per block, in two blocks. Two leaves per tree were selected from a branch located in the lower part near the trunk and facing north. The same technique was used as in Experiment 1 except that the aluminum bags were placed in the first hour of the morning and the leaves of the first measurement were bagged in the last hour of the previous day.

On the same trees, during 2014, 2015 and 2016 throughout the periods of the water stress cycles, water supply measurements were recorded for both treatments, confirming that the DI treatment did not receive any irrigation water during the stress cycles. The measures of Ψ_{st} were also taken at solar noon, using two leaves per tree, two trees per block and per treatment, which resulted in a total of 16 measures per treatment.

On two trees of each treatment, canopy transpiration was measured with a sap-flow system device which was developed and assembled at the IAS in Cordoba and described in Testi and Villalobos [46]. The system uses the compensation heat-pulse method plus the calibrated average gradient technique. Sap velocity was measured following the procedure of Green and Clothier [47], using the theoretical calibrations of Swanson and Whitfield [48], to account for the probe-induced effects of wounding. The temperature signals and the corresponding heat pulse velocities were recorded at 15 min intervals using heat-pulse instrumentation connected to a data logger (CR1000, with a multiplexer AM16/32, Campbell Scientific Inc., Logan, UT, USA).

The value of RTr (similar to Ks) is expressed as the ratio of transpiration of treatment DI to transpiration of treatment C (see irrigation treatments). The value observed in the control treatment the day before the stress cycle started was taken as the baseline reference (for normalization).

2.3. Data Analysis and Statistics

The statistical techniques employed to analyze these data were mainly linear regression and summary statistics. One-way ANOVA was also used (Experiment 1), and significant differences among treatments were evaluated with the Student-Newman-Keuls test with $p = 0.05$ using the CoStat Statistics Software (CoHort Software, Monterey, CA, USA). This type of analysis is considered not applicable when the aim is only to locate the moment for which the treatments have the largest absolute differences for the variable under analysis (as for data shown from Experiment 2), not to establish when differences between treatments appear.

3. Results

3.1. Experiment 1

Over the experimental period, the different irrigation treatments applied during 2009 to the Beja vineyard could be clearly discriminated by using Ψ_{pd} (Figure 1a); statistically significant differences at $p = 0.01$ and $p = 0.0001$ were observed respectively after DOY 203 and 217. Conversely, statistically significant differences at $p = 0.01$ and $p = 0.0001$ were observed using Ψ_{st} only after DOY 226 and DOY 230 (Figure 1b). These results suggest isohydric behavior.

The relationships between Ψ_{pd} and gs (Figure 1c) and between Ψ_{st} and gs (Figure 1d) also reveal a larger relative variation in the values observed at predawn compared to those observed at noon. A single line can be considered for Ψ_{pd}, though with high scattering for upper values of Ψ_{pd} which can be explained by the strong influence of atmospheric conditions on gs, when atmospheric stress (atmosphere causing plant stress) dominates edaphic-based stress [49]. As for $\Psi_{st,}$ there is a larger scattering of gs for average values, suggesting that initially atmospheric conditions affect both variables (Ψ_{st} and gs) but, when edaphic-based stress dominates, Ψ_{st} no longer expresses the proportion of the stomatal closure occurring (discrete distance between treatments, Figure 1d). If the degree of isohydricity can also be defined through the slope of the curve Ψ_l versus gs [50], the high slope in Figure 1d (with Ψ_{st}) supports our interpretation.

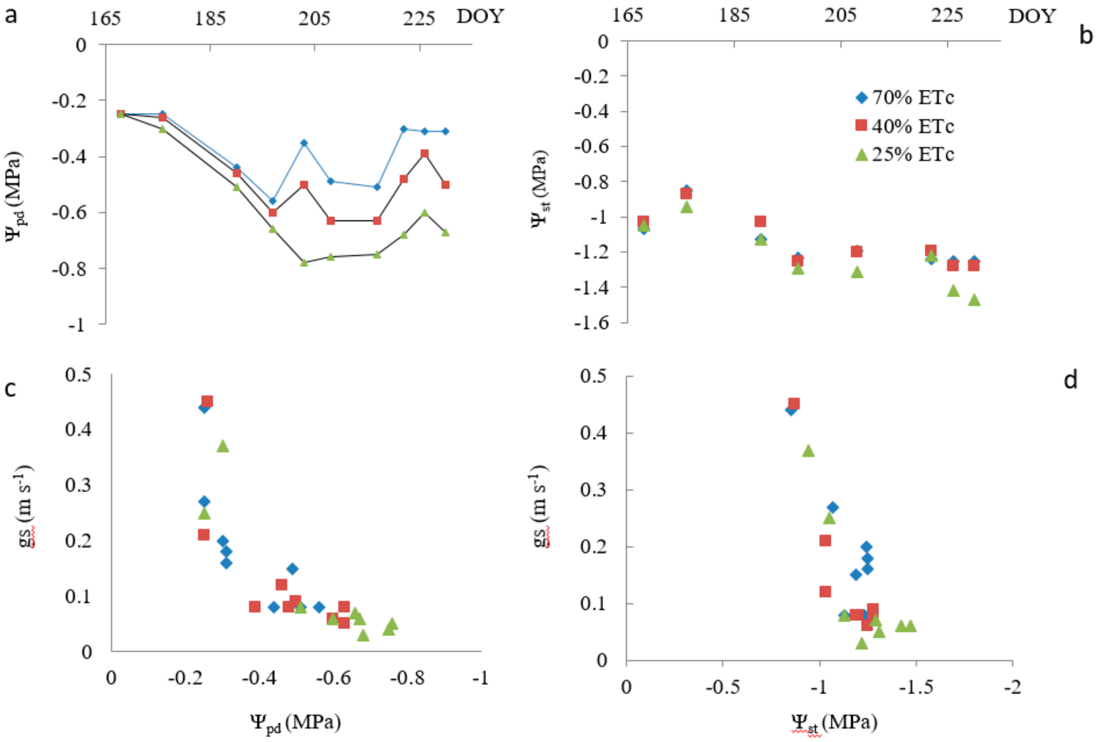

Figure 1. Seasonal course (2009) of (**a**) Ψ_{pd} and (**b**) $\Psi_{st,}$ with the relationships between those variables and noon stomatal conductance (gs); respectively (**c**,**d**), for the treatments (◊, 70% ETc; □, 40% ETc; Δ, 25% ETc) developing approximately to a weak, mild and severe water stress (see text for corresponding Ψ_{pd} ranges). The standard deviations of means are approximately within symbol width. Vineyard (Beja, Portugal).

During the short stress cycle that was imposed in 2010, the range of measured Ψ_{pd} (Figure 2a) was in agreement with values found in the literature either in the absence of water stress or with mild and severe water stress. Moreover, Ψ_{pd} was very sensitive to any irrigation applied. A strong decrease in Ψ_{pd} occurred on 10th August, possibly due to unusually hot and dry conditions during the night (min air temperature = 24.1 °C, min VPD = 1.35 kPa), which may have contributed to nocturnal transpiration.

The evolution of Ψ_{st} immediately before and during the drought stress cycle measured at 10 h, 14 h and 18 h (clock or legal time = solar time + ≈1.75 h, during summer) is presented in Figure 2b–d, respectively. Although Ψ_{st} at noon is often considered a good indicator of grapevine water status [43,51,52], this experiment suggested that this is not the case for this cultivar and under the conditions of this study, possibly due to isohydric behavior, since (again) Ψ_{st} could not discriminate between the treatments that were shown to differ by Ψ_{pd}. A similar result was found by Intrigliolo and Castel [53] for the same grapevine cultivar.

The evolution of Ψ_{st} during the day and its recovery during the afternoon were faster in CT, as expected. The range of Ψ_{st} observed is in strong disagreement with the thresholds indicated by Myburgh [54] for absence and mild water stress intensities. This can be partly attributed to the VPD influence on Ψ_{st} [52,55]. In this case, the average VPD at solar noon during the drought cycle was approximately 4.95 kPa. Moreover the high Ψ_{st} values observed during 8th August can be attributed not only to a lower VPD (3.10 kPa) but also to the heavy cloud cover observed (with ETo = 4.1 mm, whereas the average ETo during the drought cycle was 6.8 mm).

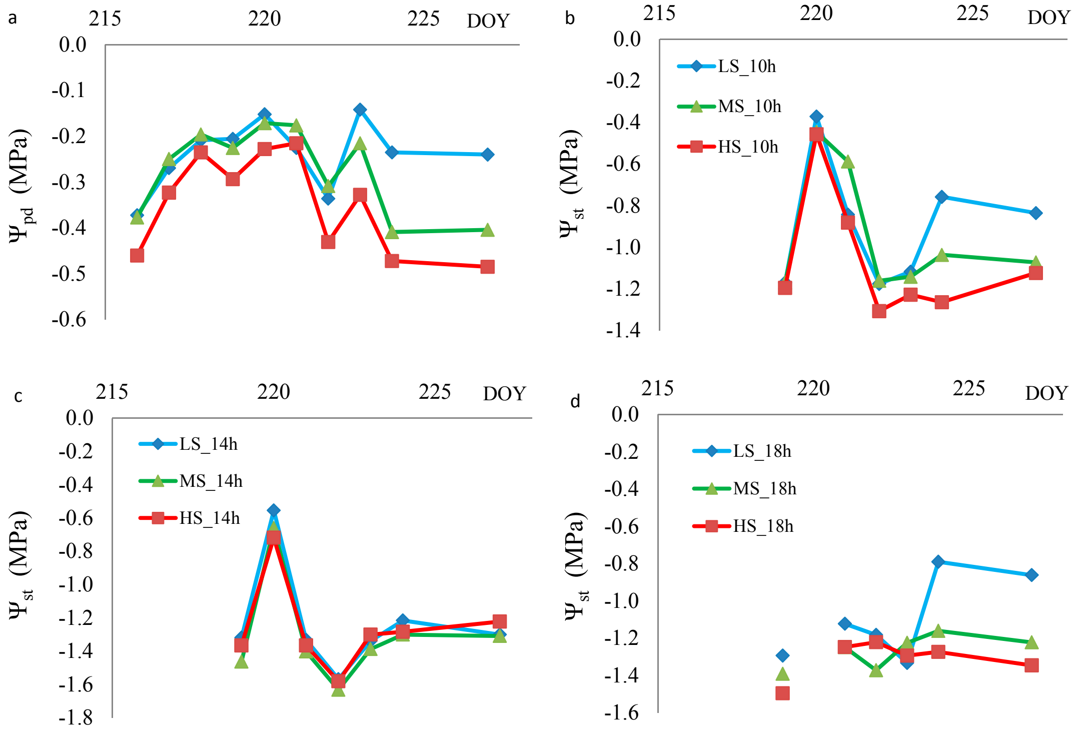

Figure 2. Observed Ψ_{pd} (**a**) and Ψ_{st} of grapevines at 10:00 a.m. (**b**); 2:00 p.m. (**c**) and 6:00 p.m. (**d**) (solar noon at ≈ 1:45 p.m.) for the treatments described (Low Stress, Medium Stress and High Stress, see text) immediately before and during the 2010 stress cycle (8th to 16th August 2010). Irrigation events during the stress cycle: see text. The standard deviations of means are within symbol width. Vineyard (Beja, Portugal).

Transpiration rates and Kc values as well as the relationship between RTr and Ψ_{pd} (Ks function) were already presented and discussed in comparison with three other vineyards, mostly rainfed [1,56], where the vineyard described here was the one suffering more stress in spite of being irrigated, with the Ks function (Ks = 1.0011 exp $-1.829\ \Psi_{pd}$, $r^2 = 0.73$) distinct from other functions obtained for the rainfed situations (lower Ks for the same Ψ_{pd}). In parallel with this Ks function for grapevines, a Ks function from Ψ_{st} for the plum orchard of Experiment 2 will be presented below.

3.2. Experiment 2

In the plum orchard at Badajoz, Spain, the minimum Ψ_{st} attained was -1.2 MPa for the DI treatment (Figure 3). Although both treatments showed the same trend in Ψ_{st}, the differences between both, around -0.2 MPa in the morning, almost doubled at noon. Other authors studying similar situations of water deficit [57,58] observed that the hours for which the differences in Ψ_{st} were more varied from day to day depended on the weather, but were usually observed roughly 1–2 h after solar noon. This greater difference does not necessarily correspond to the minimum values. In this case, we distinguished $\Psi_{st,noon}$ from Ψ_{st} because some Ψ_{st} measurements were performed during the day.

Consequently, for this cultivar, Ψ_{pd} did not seem to be as useful as Ψ_{st} as an indicator of water status. We consider that this example illustrates anisohydric behavior, due to the fact that differences in Ψ_{st} at noon were much higher than at pre-dawn, the main criteria we considered.

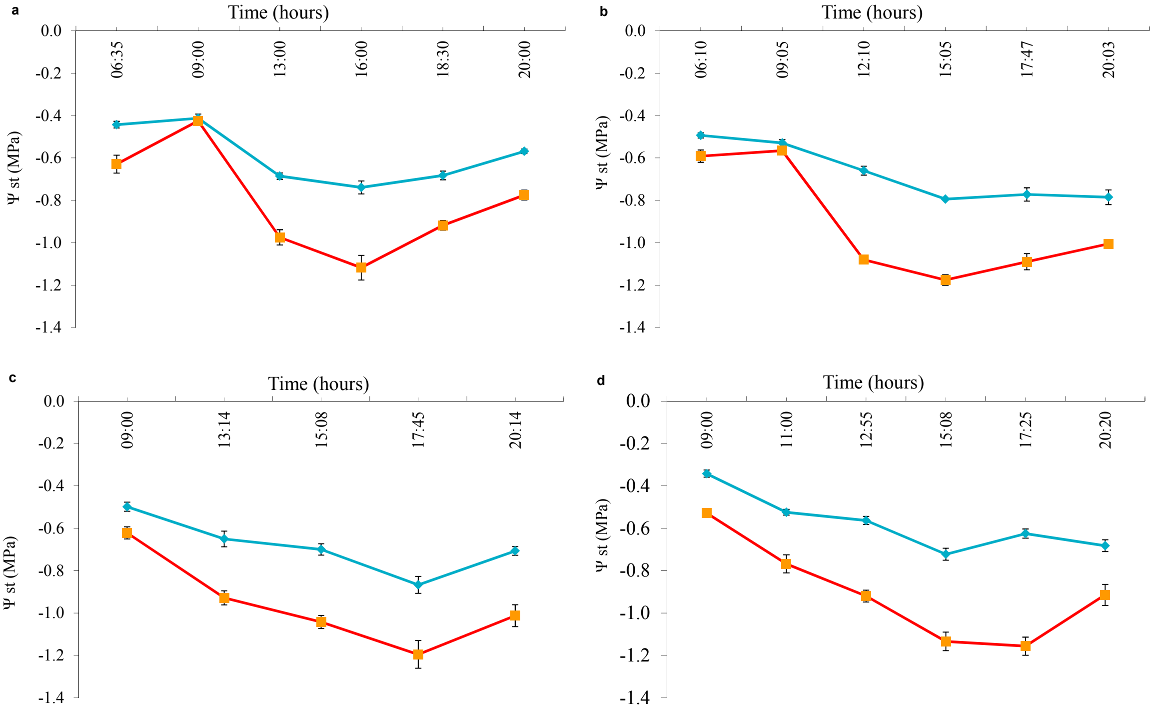

Figure 3. Plum stem water potential along the day in the control (C, Δ) and stressed plots (DI, □) for four dates: (**a**) 1 July; (**b**) 8 July; (**c**) 14 July; (**d**) 22 July. Each point represents the average of 8 trees; the vertical bars represent the standard error of each mean. Hours are legal time (solar time = legal time − 2.7 h). Plum orchard (Badajoz, Spain).

A strong relationship between $\Psi_{st,noon}$ and RTr was observed (Figure 4). The relationship between RTr and $\Psi_{st,noon}$ measured in the three years of the study developed between a maximum RTr (=1) until a threshold of −1.0 MPa was attained and, as $\Psi_{st,noon}$ decreased to −2.5 MPa, RTr decreased to 20% (RTr = 2.3767 exp −0.874 Ψ_{st}, $r^2 = 0.87$). If a linear relation was applied, $\Psi_{st,noon}$ would decrease from −1.1 MPa (Ks = 1) to around −2.7 MPa (Ks = 0).

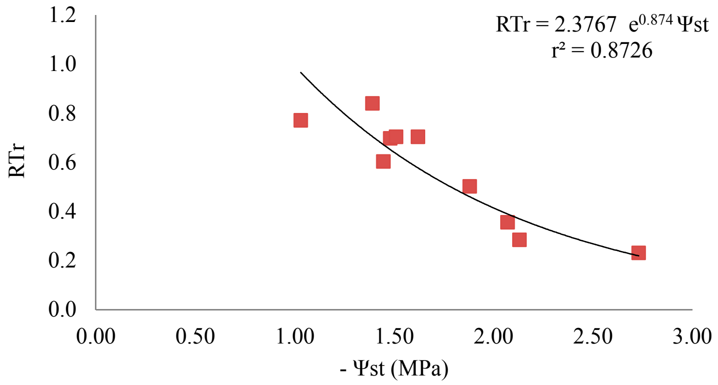

Figure 4. Relationship between Ψ_{st} measured after solar noon and daily relative transpiration (RTr) of plum. Each point is the average of two trees only for the days when Ψ_{st} was measured during the last period of each stress cycle (2014–2016).

4. Discussion

The results shown, with grapevines and plum trees, illustrated two distinct behaviors. They described the behavior of these cultivars under the environmental conditions and stress levels they experienced. In addition, the examples served to explain the criteria used in this study to distinguish between these two behaviors, isohydric versus anisohydric, which we relate to the level of isohydricity.

In order to have a general perspective of the choices made by researchers about plant stress indicators used to express water status, and their relationship with identified iso/anisohydric behavior of plants, representative studies performed with a perspective relevant for our aims, of perennial, woody agricultural crops, mostly under Mediterranean climate conditions are shown in Table 2. We focused mainly on the variables which are predominantly used in both behaviours, $\Psi_{pd,}$ $\Psi_{l,noon}$, and $\Psi_{st,noon}$. Complementary information is provided on SDV-derived variables (measured with LVDT sensors), such as the maximum daily shrinkage (MDS) or its relative value—the relative daily trunk shrinkage (RDTS), the minimum trunk diameter (MNTD), the maximum trunk diameter (MXTD), the trunk or, more generally, organ growth rate (TGR or OGR)—which is the difference between two consecutive MXTD. These are the most common SDV-derived variables, though some variations or combinations thereof have also been used. Other variables considered in these studies are mentioned. Their comparison encourages a general description, identification of general trends and inspires specific comments.

Table 2. Plant indicators used and relationship with isohydricity observed following criteria described.

Species/Cultivar	Behaviour			Plant Water Potential		SDV Derived Indexes			RTr	Other Indexes	Reference
	Iso	Aniso	Doubts	Ψ_{pd}	Ψ_{st}	MDS or RDTS	TGR	Other			
Prunus persica 'Fire-Red'		NC [2]		R	G	G	G				[59]
Prunus persica 'French'			NC	B	G				gs [1]		[60]
Prunus persica 'Cal Red'	*			G	B					gs, LT [3]	[58]
Prunus persica 'H30'	*			G		RDTS				Tr, gs relat, θs	[61]
Actinidia deliciosa 'Deliciosa'	*			G						gs, A, Tr	[62]
Prunus persica 'O'Henry'			*	G	G	R		MXTD MNTD		θs [4]	[63]
Vitis vinifera 'Trincadeira'	*			G	B					Tr, gs,	[64]
Prunus persica 'Andros'		*		G	G	G	G				[9]
Malus domestica 'Golden delicious'	*			B	G	G			G	gs relat	[65]
Vitis vinifera 'Tempranillo'	*			G	B					gs	[66]
Prunus salicina 'Black Gold'			NC		G	R [5]					[67]
Diospyros kaki. 'Rojo Brillante'		*	NC		R	R				gs	[10]
Punica granatum 'Mollar de Elche'	*				G	R	B				[68]
Prunus persica 'Flordastar'			NC		B	G					[11]
Olea europea 'Arbequina'	*			G		B [8]	B [8]	D_{MXTD}/MXTD		Tr, θs	[69]
Punica granatum 'Mollar de Elche'	*,[7]			G	B					gs	[57]
Prunus persica 'Silver King'	*			G						Tr	[70]
Actinidia deliciosa 'Hayward'		*		B	G	R		MDS (1-OGR) [6]		gs, θs	[71]

* Apparent behavior from the results presented by authors; [1] A relationship of Ψ_{pd} or Ψ_{st} difference versus relative gs or RTr was used; [2] NC = Not clear; plant does not have a clear behavior but more anisohydric, or G = good, R = regular, B = bad; [3] LT = leaf temperature; [4] Best is daily variations in θ_s; [5] SDV regular (RDTS required); [6] In agreement with suggestion [9] of combining both indexes; [7] Tends to anisohydric, towards the end of stress cycle; [8] Implicitly.

In general, it is claimed that the variables (indicators) most closely related with important biological processes should be selected as they are better indicators in relation to growth processes (e.g., [9]). Ψ_{st} in this respect is often recommended. MDS was shown to depend on seasonal changes in trunk growth and both MDS and Ψ_{st} were valued by Marsal et al. [9] for accounting for day-to-day variations in diurnal atmospheric demand, expressed in general by ETo.

4.1. Plant Water Status Indicators Versus Water Stress

An increase in ETo, which can possibly cause atmospheric stress, can hardly be solved by irrigation except when there is an important percentage of wet soil surface (e.g., by mini sprinklers), and in stands with low aerodynamic conductance [49]. If Ψ_{st} decreases due to changes in ETo, wetting the soil in a drip-irrigated orchard would apparently have a negligible effect on decreasing VPD anyway (and increasing gs and carbon exchanges).

Irrigation aims first at decreasing or preventing edaphic-based stress. Consequently, the value of any variable considered for scheduling irrigation that is heavily influenced by diurnal atmospheric stress can be controversial in its effectiveness for irrigation scheduling decisions.

Several researchers (e.g., [11]) have compared the earliness of water stress detection by different indicators versus soil water content (θ_s) but have sometimes not related it to the readily available water (RAW) concept. This possibly leads to misinterpreting apparent late reactions of several indicators versus θ_s (since no water stress is expected while the soil water is within the RAW limits).

Like peach trees, kiwi (*Actinidia deliciosa*), grapevines, and olive (*Olea europea*) trees also displayed different behaviors (isohydricity) depending on the particular cultivar in question. However, the simple criteria used here for irrigation scheduling would seem inadequate for the complex interpretation required when dealing with olive tree cultivars. According to Ennajeh et al. [72], even if transpiration can also be significantly reduced under stress due to stomatal closure, Ψ_l can be extremely low in relation to most other tree species as a result of the ability of olive trees to transfer water from tissues to the xylem sap.

4.2. Use of Water Stress Indicators

A study with peach [63] with an intermediate behavior showed important variations in TGR and MDS, $\Psi_{st,}$ Ψ_l and Ψ_{pd}. The authors did not report any stomatal conductance measurements. The way in which these authors and others that followed valued the different indicators was based on relative values. Relative values were relevant in some cases and will be used in this discussion only for flux,conductance and SDV derived variables, but not for potentials. However, there is a limitation in that they require a well-watered control used as reference. For instance, due to the observed effects of environmental atmospheric conditions on MDS, Ferreira et al. [61] did not use MDS directly but RDTS to evaluate water stress in peach.

Some studies [4,67,73] have demonstrated that atmospheric conditions have significant effects on Ψ_{st} and/or especially MDS, with relationships that change with the carbon status of the plant, dependent for instance on the pre- or postharvest condition. Intrigliolo and Castel [67] also concluded that MDS should be considered only in relative terms (as RDTS).

A review of a large collection of Spanish studies on the use of SDV, Ψ_{st} and Ψ_{leaf} for irrigation scheduling related to different environmental variables [13] also implicitly supported this perspective, even suggesting that MDS (or RDTS, later called in that study the MDS signal intensity) should be combined with other water stress indicators. Intrigliolo et al. [68] showed that the MDS difference between treatments, with pomegranate, increased with stress and then tended to stabilize or even decrease. This was also observed by other research [13,61]. The values of $\Psi_{st,noon}$ were closely related to other indicators of plant stress [74–77]. In some cases, this indicator has been related to the reduction in transpiration (RTr or Ks), as in Figure 4. Anisohydric mechanisms apparently caused greater Tr rates at noon, which was reflected in the fact that the most commonly used indicators of stress were expected to be involved with changes in plant tissue volume. The SDV-derived indicators were widely described in the literature as being the most suitable for determination of the water status of plant with anisohydric behavior and therefore for irrigation scheduling [13,78,79]. These indexes seem to be among the most popular plant water stress indicators, with the advantage of providing a continuous data-set over time [5,80]. This applies especially to young trees where OGR is one of the earliest responses to plant water stress [81]. The literature suggests that in plants with anisohydric behavior, MNTD and MDS are the most commonly used indexes, although a combination of trunk and tree organ measurements is also effective [71]. However, MXTD seems inadequate for this purpose [63,82]. By contrast, tests performed on isohydric species showed a lack of use of this type of indicator. Intrigliolo et al. [68] showed how the use of TGR was unsuitable as a measure to determine plant water status in pomegranate [67]. The same conclusion was reached for peach [83].

In summary, water potential measurements have been widely used in many studies. The high levels of measurement repeatability and reliability have made them popular for irrigation scheduling, although some authors [9,63] have pointed out that in anisohydric species these indicators are not as reliable as SDV-derived indexes, especially Ψ_{pd}, where no differences were found between species under deficit irrigation treatment. Conversely, Ψ_{pd} is the most commonly used and most highly valued variable to quantify plant water status in plants with isohydricbehaviour.

The present discussion focused on authors who use stress indicators for irrigation management (Table 2) and showed that there has been a tendency to use a certain type of indicator according to the behavior of the case-studies considered: (1) all the studies on plants with isohydric behavior whereby were measured Ψ_{pd} showed this variable performed well as a water stress indicator; (2) all the studies on species with isohydric behavior which measured Ψ_{st} reported that this indicator did not perform well; (3) a few studies on species with isohydric behavior which analyzed SDV reported satisfactory results with RDTS or D_{MXTD}/MXTD (difference of MXTD divided by the value observed for a well-watered control). In relation to anisohydric behavior, there has been a tendency to obtain a better performance using SDV-derived indexes than with isohydric cultivars, especially with MDS. In general, Ψ_{st} also performs well with all anisohydric species or in cases where the behavior is not clear. However, Ψ_{st} performs badly with isohydric species, with the sole exception of pomegranate [68]. These results confirm our hypothesis. We should stress that apparently the choices made by researchers for measurements or the presentation of results often seem to be made having already taken this concept into account, even when not explicitly.

Ks functions where Ks is estimated from SWD have been used but, there are no studies of relationships between Ks and plant indicators. This may be attributed to the use of plant water status indicators which are often linked to a feed-back approach which does not usually require Ks estimates. Consequently, it is difficult to provide a summary of the use of such Ks functions from plant indicators.

4.3. When to Use Predawn or Noon Stem Water Potential

In conclusion, our results and those of others suggested that Ψ_{st} performs better and therefore is a preferred stress indicator in plants with anisohydric behavior, while in plants with isohydric behavior, Ψ_{pd} is generally preferred.

It is important to stress that the validity of these indicators depends not only on isohydric versus anisohydric behavior, but also on the stress level to which plants are subjected, as several authors [57,63,64] have demonstrated. Although SDV seemed to provide more interesting indicators for anisohydric species, the sensitivity of the derived indicator also changed as the range of water stress level varied.

It is clear from these observations that the behavior also depends on the cultivar in question, as demonstrated for instance for grapevines and peach (Table 2). Associating isohydricity with species (e.g., ring-porous versus diffuse-porous wood) is apparently not supported by these results.

If the choice of SDV-derived indexes is related to isohydricity, possible guidelines for these indicators could be determined from further in-depth analyses in future studies.

The differences between isohydric and anisohydric behavior complicate the choice and use of a stress indicator in a particular cultivar. A prior study of plant behavior with environmental changes is recommended to establish which variable provides the best information, unless a collection of data on different indicators is already available.

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References

1. Ferreira, M.I. Stress Coefficients for Soil Water Balance Combined with Water Stress Indicators for Irrigation Scheduling of Woody Crops. *Horticulturae* **2017**, *3*, 38. [CrossRef]
2. Katerji, N.; Hallaire, M. Les grandeurs de référence utilisables dans l'étude de l'alimentation en eau des cultures. *Agronomie* **1984**, *4*, 999–1008. [CrossRef]
3. Chalmers, D.J.; Mitchell, P.D.; Vanheek, L. Control of peach tree growth and productivity by regulated water supply, tree density and summer pruning. *J. Am. Soc. Hortic. Sci.* **1981**, *106*, 307–312.
4. Ortuño, M.F.; Conejero, W.; Moreno, F.; Moriana, A.; Intrigliolo, D.S.; Biel, C.; Mellisho, C.D.; Pérez-Pastor, A.; Domingo, R.; Ruiz-Sánchez, M.C.; et al. Could trunk diameter sensors be used in woody crops for irrigation scheduling? A review of current knowledge and future perspectives. *Agric. Water Manag.* **2010**, *97*, 1–11. [CrossRef]
5. Goldhamer, D.A.; Fereres, E. Irrigation scheduling protocols using continuously recorded trunk diameter measurements. *Irrig. Sci.* **2001**, *20*, 115–125. [CrossRef]
6. Goldhamer, D.A.; Fereres, E. Irrigation scheduling of almond trees with trunk diameter sensors. *Irrig. Sci.* **2004**, *23*, 11–19. [CrossRef]
7. Jones, H.G. Irrigation scheduling: Advantages and pitfalls of plant-based methods. *J. Exp. Bot.* **2004**, *55*, 2427–2436. [CrossRef] [PubMed]
8. Fernández, J.E. Plant-Based Methods for Irrigation Scheduling of Woody Crops. *Horticulturae* **2017**, *3*, 35. [CrossRef]
9. Marsal, J.; Gelly, M.; Mata, M.; Arbonés, A.; Rufat, J.; Girona, J. Phenology and drought affects the relationship between daily trunk shrinkage and midday stem water potential of peach trees. *J. Hortic. Sci. Biotechnol.* **2002**, *77*, 411–417. [CrossRef]
10. Badal, E.; Buesa, I.; Guerra, D.; Bonet, L.; Ferrer, P.; Intrigliolo, D.S. Maximum diurnal trunk shrinkage is a sensitive indicator of plant water, stress in Diospyros kaki (Persimmon) trees. *Agric. Water Manag.* **2010**, *98*, 143–147. [CrossRef]
11. Conejero, W.; Mellisho, C.D.; Ortuño, M.F.; Moriana, A.; Moreno, F.; Torrecillas, A. Using trunk diameter sensors for regulated deficit irrigation scheduling in early maturing peach trees. *Environ. Exp. Bot.* **2011**, *71*, 409–415. [CrossRef]
12. De Schepper, V.; van Dusschoten, D.; Copini, P.; Jahnke, S.; Steppe, K. MRI links stem water content to stem diameter variations in transpiring trees. *J. Exp. Bot.* **2012**, *63*, 2645–2653. [CrossRef] [PubMed]
13. Fernández, J.E.; Cuevas, M.V. Irrigation scheduling from stem diameter variations: A review. *Agric. For. Meteorol.* **2010**, *150*, 135–151. [CrossRef]

14. Stegman, E.C.; Schiele, L.H.; Bauer, A. Plant water stress criteria for irrigation scheduling. *Trans. ASAE* **1976**, *19*, 0850–0855. [CrossRef]
15. Allen, R.G.; Pereira, L.S.; Raes, D.; Smith, M. *Crop Evapotranspiration-Guidelines for Computing Crop Water Requirements-FAO Irrigation and Drainage Paper 56*; FAO: Rome, Italy, 1998; Volume 300, p. D05109.
16. Jarvis, P.G. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **1976**, *273*, 593–610. [CrossRef]
17. Hinckley, T.M.; Duhme, F.; Hinckley, A.R.; Richter, H. Water relations of drought hardy shrubs: Osmotic potential and stomatal reactivity. *Plant Cell Environ.* **1980**, *3*, 131–140.
18. Hugalde, I.P.; Vila, H.F. Comportamiento isohídrico o anisohídrico en vides . . . :¿ Una controversia sin fin? *RIA Rev. Investig. Agropecu.* **2014**, *40*, 75–82.
19. Jones, H.G. Physiological aspects of the control of water status in horticultural crops. *HortScience* **1990**, *25*, 19–26.
20. Lovisolo, C.; Perrone, I.; Carra, A.; Ferrandino, A.; Flexas, J.; Medrano, H.; Schubert, A. Drought-induced changes in development and function of grapevine (*Vitis* spp.) organs and in their hydraulic and non-hydraulic interactions at the whole-plant level: A physiological and molecular update. *Funct. Plant Biol.* **2010**, *37*, 98–116.
21. Chaves, M.M.; Zarrouk, O.; Francisco, R.; Costa, J.M.; Santos, T.; Regalado, A.P.; Lopes, C.M. Grapevine under deficit irrigation: Hints from physiological and molecular data. *Ann. Bot.* **2010**, *105*, 661–676. [CrossRef] [PubMed]
22. Domec, J.C.; Johnson, D.M. Does homeostasis or disturbance of homeostasis in minimum leaf water potential explain the isohydric versus anisohydric behavior of *Vitis vinifera* L. cultivars? *Tree Physiol.* **2012**, *32*, 245–248. [CrossRef] [PubMed]
23. Stocker, O. Die Abhängigkeit des transpiration von den unweltfaktoren. In *Encyclopedia of Plant Physiology*; Ruhland, W., Ed.; Springer-Verlag: Berlin, Germany, 1956; Volume 3.
24. Konings, A.G.; Gentine, P. Global variations in ecosystem-scale isohydricity. *Glob. Chang. Biol.* **2017**, *23*, 891–905. [CrossRef] [PubMed]
25. Schultz, H.R. Differences in hydraulic architecture account for near-isohydric and anisohydric behaviour of two field-grown *Vitis vinifera* L. cultivars during drought. *Plant Cell Environ.* **2003**, *26*, 1393–1405. [CrossRef]
26. Rogiers, S.Y.; Greer, D.H.; Hutton, R.J.; Clarke, S.J. Transpiration efficiency of the grapevine cv. Semillon is tied to VPD in warm climates. *Ann. Appl. Biol.* **2011**, *158*, 106–114. [CrossRef]
27. Domec, J.C.; Noormets, A.; King, J.S.; Sun, G.E.; McNulty, S.G.; Gavazzi, M.J.; Bloggs, J.L.; Treasure, E.A. Decoupling the influence of leaf and root hydraulic conductances on stomatal conductance and its sensitivity to vapour pressure deficit as soil dries in a drained loblolly pine plantation. *Plant Cell Environ.* **2009**, *32*, 980–991. [CrossRef] [PubMed]
28. Lovisolo, C.; Hartung, W.; Schubert, A. Whole-plant hydraulic conductance and root-to-shoot flow of abscisic acid are independently affected by water stress in grapevines. *Funct. Plant Biol.* **2002**, *29*, 1349–1356. [CrossRef]
29. Intrigliolo, D.S.; Castel, J.R. Usefulness of diurnal trunk shrinkage as a water stress indicator in plum trees. *Tree Physiol.* **2006**, *26*, 303–311. [CrossRef] [PubMed]
30. Simonneau, T.; Habib, R.; Goutouly, J.P.; Huguet, J.G. Diurnal changes in stem diameter depend upon variations in water content: Direct evidence in peach trees. *J. Exp. Bot.* **1993**, *44*, 615–621. [CrossRef]
31. Jarvis, P.G. Water transfer in plants. In *Heat and Mass Transfer in the Plant Environment*; De Vries, D., Afgan, N.H., Eds.; John Wiley & Sons Inc.: New York, NY, USA, 1975; Chapter 1; pp. 369–394.
32. Scholz, F.C.; Bucci, S.J.; Goldstein, G.; Meinzer, F.C.; Franco, A.C.; Miralles-Wilhelm, F. Temporal dynamics of stem expansion and contraction in savanna trees: Withdrawal and recharge of stored water. *Tree Physiol.* **2008**, *28*, 469–480. [CrossRef] [PubMed]
33. Meinzer, F.C.; Johnson, D.M.; Lachenbruch, B.; McCulloh, K.A.; Woodruff, D.R. Xylem hydraulic safety margins in woody plants: Coordination of stomatal control of xylem tension with hydraulic capacitance. *Funct. Ecol.* **2009**, *23*, 922–930. [CrossRef]
34. Meinzer, F.C.; Woodruff, D.R.; Marias, D.E.; Mcculloh, K.A.; Sevanto, S. Dynamics of leaf water relations components in co-occurring iso- and anisohydric conifer species. *Plant Cell Environ.* **2014**, *37*, 2577–2586. [CrossRef] [PubMed]

35. Meinzer, F.C.; Woodruff, D.R.; Marias, D.E.; Smith, D.D.; McCulloh, K.A.; Howard, A.R.; Magedman, A.L. Mapping 'hydroscapes' along the iso-to anisohydric continuum of stomatal regulation of plant water status. *Ecol. Lett.* **2016**, *19*, 1343–1352. [CrossRef] [PubMed]
36. Garcia-Forner, N.; Adams, H.D.; Sevanto, S.; Collins, A.D.; Dickman, L.T.; Hudson, P.J.; Zeppel, M.J.B.; Jenkins, M.W.; Powers, H.; Martínez-Vilalta, J.; et al. Responses of two semiarid conifer tree species to reduced precipitation and warming reveal new perspectives for stomatal regulation. *Plant Cell Environ.* **2016**, *39*, 38–49. [CrossRef] [PubMed]
37. Martínez-Vilalta, J.; Garcia-Forner, N. Water potential regulation, stomatal behaviour and hydraulic transport under drought: Deconstructing the isohydric and anisohydric concept. *Plant Cell Environ.* **2016**, *40*, 962–976. [CrossRef] [PubMed]
38. Lavoie-Lamoureux, A.; Sacco, D.; Risse, P.A.; Lovisolo, C. Factors influencing stomatal conductance in response to water availability in grapevine: A meta-analysis. *Physiol. Plant.* **2017**, *159*, 468–482. [CrossRef] [PubMed]
39. McDowell, N.; Pockman, W.T.; Allen, C.D.; Breshears, D.D.; Cobb, N.; Kolb, T.; Plaut, J.; Sperry, J.; West, A.; Williams, D.G.; et al. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytol.* **2008**, *178*, 719–739. [CrossRef] [PubMed]
40. Martínez-Vilalta, J.; Poyatos, R.; Aguadé, D.; Retana, J.; Mencuccini, M. A new look at water transport regulation in plants. *New Phytol.* **2014**, *204*, 105–115. [CrossRef] [PubMed]
41. Roman, D.T.; Novick, K.A.; Brzostek, E.R.; Dragoni, D.; Rahman, F.; Phillips, R.P. The role of isohydric and anisohydric species in determining ecosystem-scale response to severe drought. *Oecologia* **2015**, *179*, 641–654. [CrossRef] [PubMed]
42. Klein, T. The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. *Funct. Ecol.* **2014**, *28*, 1313–1320. [CrossRef]
43. Choné, X.; Van Leeuwen, C.; Dubourdieu, D.; Gaudillère, J.-P. Stem water potential is a sensitive indicator of grapevine water status. *Ann. Bot.* **2001**, *87*, 477–483. [CrossRef]
44. Riou, C.; Payan, J.C. Outils de gestion de l'eau en vignoble méditerranéen. Application du bilan hydrique au diagnostique du stress hydrique de la vigne. *12 Journ. GESCO, Journ. Prof. Gest. L'eau Dans Vign.* **2001**, 125–133.
45. Shackel, K.A.; Ahmadi, H.; Biasi, A.W.; Buchner, R.; Goldhamer, D.; Gurusinghe, S.; Hasey, J.; Kester, D.B.; Krueger, B.; Lampinen, B.; et al. Plant water status as an index of irrigation need in deciduous fruit trees. *Hort Technol.* **1997**, *7*, 23–29.
46. Testi, L.; Villalobos, F.J. New approach for measuring low sap velocities in trees. *Agric. For. Meteorol.* **2009**, *149*, 730–773. [CrossRef]
47. Green, S.R.; Clothier, B.E. Water use of kiwifruit vines and apple trees by the heat-pulse technique. *J. Exp. Bot.* **1998**, *39*, 115–123. [CrossRef]
48. Swanson, R.H.; Whitfield, D.W.A. A numerical analysis of heat pulse velocity theory and practice. *J. Exp. Bot.* **1981**, *32*, 221–239. [CrossRef]
49. Ferreira, M.I.; Katerji, N. Is stomatal conductance in a tomato crop controlled by soil or atmosphere? *Oecologia* **1992**, *92*, 104–107. [CrossRef] [PubMed]
50. Matheny, A.M.; Mirfenderesgi, G.; Bohrer, G. Trait-based representation of hydrological functional properties of plants in weather and ecosystem models. *Plant Divers.* **2017**, *39*, 1–12. [CrossRef]
51. Patakas, A.; Noitsakis, B.; Chouzouri, A. Optimization of irrigation water use in grapevines using the relationship between transpiration and plant water status. *Agric. Ecosyst. Environ.* **2005**, *106*, 253–259. [CrossRef]
52. Olivo, N.; Girona, J.; Marsal, J. Seasonal sensitivity of stem water potential to vapour pressure deficit in grapevine. *Irrig. Sci.* **2009**, *27*, 175–182. [CrossRef]
53. Intrigliolo, D.S.; Castel, J.R. Evaluation of grapevine water status from trunk diameter variations. *Irrig. Sci.* **2007**, *26*, 49–59. [CrossRef]
54. Myburgh, P.A. Response of *Vitis vinifera* L. cv. Merlot to low frequency drip irrigation and partial root zone drying in the Western Cape Coastal Region—Part I. Soil and plant water status. *S. Afr. J. Enol. Vitic.* **2011**, *32*, 89–103. [CrossRef]
55. Williams, L.E.; Baeza, P. Relationships among ambient temperature and vapor pressure deficit and leaf and stem water potentials of fully irrigated, field-grown grapevines. *Am. J. Enol. Vitic.* **2007**, *58*, 173–181.

56. Ferreira, M.I.; Silvestre, J.; Conceição, N.; Malheiro, C. Crop and stress coefficients in rainfed and deficit irrigation vineyards using sap flow techniques. *Irrig. Sci.* **2012**, *30*, 433–444. [CrossRef]
57. Rodríguez, P.; Mellisho, C.D.; Conejero, W.; Cruz, Z.N.; Ortuno, M.F.; Galindo, A.; Torrecillas, A. Plant water relations of leaves of pomegranate trees under different irrigation conditions. *Environ. Exp. Bot.* **2012**, *77*, 19–24. [CrossRef]
58. Girona, J.; Mata, M.; Goldhamer, D.A.; Johnson, R.S.; DeJong, T.M. Patterns of soil and tree water status and leaf functioning during regulated deficit irrigation scheduling in peach. *J. Am. Soc. Hortic. Sci.* **1993**, *118*, 580–586.
59. Selles, G.; Berger, A. Physiological indicators of plant water status as criteria for irrigation scheduling. *Acta Hortic.* **1989**, *278*, 87–100. [CrossRef]
60. McCutchan, H.; Shackel, K.A. Stem-water potential as a sensitive indicator of water stress in prune trees (*Prunus domestica* L. cv. French). *J. Am. Soc. Hortic. Sci.* **1992**, *117*, 607–611.
61. Ferreira, M.I.; Valancogne, C.; Daudet, F.-A.; Ameglio, T.; Pacheco, C.A.; Michaelsen, J. Evapotranspiration and crop-water relations in a peach orchard. In Proceedings of the International Conference on "Evapotranspiration and Irrigation Scheduling", San Antonio, TX, USA, 3–6 November 1996; pp. 61–69.
62. Gucci, R.; Massai, R.; Xiloyannis, C.; Flore, J.A. The effect of drought and vapour pressure deficit on gas exchange of young kiwifruit (*Actinidia deliciosa* var. deliciosa) vines. *Ann. Bot.* **1996**, *77*, 605–613. [CrossRef]
63. Goldhamer, D.A.; Fereres, E.; Mata, M.; Girona, J.; Cohen, M. Sensitivity of continuous and discrete plant and soil water status monitoring in peach trees subjected to deficit irrigation. *J. Am Soc. Hortic. Sci.* **1999**, *124*, 437–444.
64. Silvestre, J.; Ferreira, M.I. Efects of irrigation on transpiration and water relations of vineyards, in the Teja Valley (central Portugal). *Acta Hortic.* **2000**, *537*, 305–312. [CrossRef]
65. Naor, A.; Cohen, S. Sensitivity and variability of maximum trunk shrinkage, midday stem water potencial, and transpiration rate in response to withholding irrigation from field-grown apple trees. *HortScience* **2003**, *38*, 547–551.
66. Malheiro, A.C.; Gonçalves, I.N.; Fernandes-Silva, A.A.; Silvestre, J.C.; Conceição, N.S.; Paço, T.A.; Ferreira, M.I. Relationships between relative transpiration of grapevines and plant and soil water status in Portugal's Douro wine region. *Acta Hortic.* **2011**, *922*, 261–267. [CrossRef]
67. Intrigliolo, D.S.; Castel, J.R. Effects of regulated deficit irrigation on growth and yield of young Japanese plum trees. *J. Hortic. Sci. Biotechnol.* **2005**, *80*, 177–182. [CrossRef]
68. Intrigliolo, D.S.; Puerto, H.; Bonet, L.; Alarcón, J.J.; Nicolas, E.; Bartual, J. Usefulness of trunk diameter variations as continuous water stress indicators of pomegranate (*Punica granatum*) trees. *Agric. Water Manag.* **2011**, *98*, 1462–1468. [CrossRef]
69. Ferreira, M.I.; Conceição, N.; Pacheco, C.A.; Häusler, M. Análise de indicadores de desconforto hídrico durante ciclos de stress num olival intensivo no Alentejo. *Atas Port. Hortic.* **2012**, *21*, 217–226.
70. Paço, T.; Ferreira, M.I.; Pacheco, C.A. Scheduling peach orchard irrigation in water stress conditions: Use of relative transpiration and predawn leaf water potential. *Fruits* **2013**, *68*, 147–158. [CrossRef]
71. Silva, R.; Ferreira, M.I. A new microdendrometric index to quantify water status in kiwifruit. *Acta Hortic.* **2014**, *1038*, 43–50.
72. Ennajeh, M.; Tounekti, T.; Vadel, A.M.; Khemira, H.; Cochard, H. Water relations and drought-induced embolism in olive (*Olea europaea*) varieties 'Meski' and 'Chemlali' during severe drought. *Tree Physiol.* **2008**, *28*, 971–976. [CrossRef] [PubMed]
73. Fereres, E.; Goldhamer, D. Suitability of stem diameter variations and water potential as indicators for irrigation scheduling of almond trees. *J. Hortic. Sci. Biotechnol.* **2003**, *78*, 139–144. [CrossRef]
74. Rieger, M.; Duemmel, M.J. Comparison of drought resistance among Prunus species from divergent habitats. *Tree Physiol.* **1992**, *11*, 369–380. [CrossRef] [PubMed]
75. Lankes, C. Effect of water stress on transpiration and CO_2 gas exchange of the apple leaf and fruit. *Acta Hortic.* **1985**, *171*, 305–314.
76. Jorba, J.; Tapia, L.; Sant, D. Photosynthesis, leaf water potential, and stomatal conductance in *Olea europaea* under wet and drought conditions. *Acta Hortic.* **1984**, *171*, 237–246. [CrossRef]
77. Tan, C.S.; Buttery, B.R. Response of stomatal conductance, transpiration, photosynthesis, and leaf water potential in peach seedlings to different watering regimes. *HortScience* **1982**, *17*, 222–223.

78. Doltra, J.; Oncins, J.A.; Bonany, J.; Cohen, M. Evaluation of plant-based water status indicators in mature apple trees under field conditions. *Irrig. Sci.* **2007**, *25*, 351–359. [CrossRef]
79. Velez, J.E.; Intrigliolo, D.S.; Castel, J.R. Scheduling deficit irrigation of citrus trees with maximum daily trunk shrinkage. *Agric. Water Manag.* **2007**, *90*, 197–204. [CrossRef]
80. Huguet, J.G. Appréciation de l'état hydrique d'une plante à partir des variations micrométriques de la dimension des fruits ou des tiges au cours de la journée. *Agronomie* **1985**, *5*, 733–741. [CrossRef]
81. Nortes, P.A.; Pérez-Pastor, A.; Egea, G.; Conejero, W.; Domingo, R. Comparison of changes in stem diameter and water potential values for detecting water stress in young almond trees. *Agric. Water Manag.* **2005**, *77*, 296–307. [CrossRef]
82. Li, S.H.; Huguet, J.G.; Bussi, C. Irrigation scheduling in a mature peach orchard using tensiometers and dendrometers. *Irrig. Drain. Syst.* **1989**, *3*, 1–12. [CrossRef]
83. Remorini, D.; Massai, R. Comparison of water status indicators for young peach trees. *Irrig. Sci.* **2003**, *22*, 39–46.