

## Research Paper

Multi-scale assessment of plant water status in *Diospyros kaki* grafted onto *D. lotus* and *D. virginiana* under water deficit

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## ARTICLE INFO

## Keywords:

*Diospyros kaki*

Drought

Stomatal behaviour

Trunk water potential ( $\Psi_{\text{trunk}}$ )

Sap flow (SF)

## ABSTRACT

This study analyses drought response strategies in persimmon rootstocks by evaluating the physiological responses of persimmon (*Diospyros kaki* Thunb.) cv. 'Rojo Brillante' trees grafted onto *D. lotus* and *D. virginiana* under summer water conditions in the SE of Spain. Fully irrigated trees (100% ET<sub>c</sub>) were compared with trees subjected to irrigation restriction until midday stem water potential ( $\Psi_{\text{stem}}$ ) reached  $-1.6$  MPa (severe water deficit). Measurements of soil water content, trunk water potential ( $\Psi_{\text{trunk}}$ ) and sap flow were monitored, together with temporal determinations of  $\Psi_{\text{stem}}$ , midday leaf water potential and leaf gas exchange. In addition, UAV-based thermal and multispectral indicators were obtained at peak water stress. Our results revealed contrasting hydraulic strategies between rootstocks. *D. lotus* showed physiological traits consistent with a more anisohydric-like response, with rapid decreases in  $\Psi_{\text{stem}}$  and  $\Psi_{\text{trunk}}$ , whilst maintaining relatively stable leaf gas exchange. In contrast, *D. virginiana* exhibited a more conservative stomatal regulation, suggesting a more isohydric-like behaviour, under water deficit conditions. Among the plant-based indicators,  $\Psi_{\text{trunk}}$  showed the highest sensitivity (S) and reliability for detecting drought stress. Sap flow measurements reflected transpiration dynamics, but with lower sensitivity, mainly due to differences in canopy size between rootstocks. UAV-derived spectral indices were primary driven by structural differences between rootstocks, whilst canopy temperature was the most sensitive remote sensing indicator to water deficit. These findings suggest that drought detectability in persimmon is strongly driven by rootstock-dependent hydraulic behaviour, highlighting  $\Psi_{\text{trunk}}$  as a reliable plant-based indicator of persimmon water status under the conditions evaluated in this whole-tree transpiration study. Additionally, *D. virginiana* may represent a promising rootstock option under semi-arid Mediterranean conditions.

## List of abbreviations

|                      |                                   |
|----------------------|-----------------------------------|
| $\Theta_v$           | soil water content                |
| VPD                  | vapour pressure deficit           |
| ET <sub>0</sub>      | reference crop evapotranspiration |
| K <sub>c</sub>       | crop coefficient                  |
| ET <sub>c</sub>      | crop evapotranspiration           |
| $\Psi_{\text{leaf}}$ | leaf water potential              |
| $\Psi_{\text{stem}}$ | stem water potential              |
| P <sub>n</sub>       | net photosynthesis                |
| g <sub>s</sub>       | stomatal conductance              |

|                       |                                        |
|-----------------------|----------------------------------------|
| WUE <sub>T</sub>      | transpiration efficiency               |
| SF                    | sap flow                               |
| $\Psi_{\text{trunk}}$ | trunk water potential                  |
| MTs                   | trunk microtensiometers                |
| SHB                   | stem heat balance                      |
| TDR                   | Time Domain Reflectometry              |
| UAV                   | unmanned aerial vehicles               |
| T <sub>c</sub>        | canopy temperature                     |
| VIS-NIR               | visible-near infrared                  |
| NDVI                  | Normalized Difference Vegetation Index |
| NDRE                  | Normalized Difference Red-Edge Index   |

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<https://doi.org/10.1016/j.scienta.2026.115030>

Received 21 April 2026; Received in revised form 9 July 2026; Accepted 9 July 2026

Available online 23 July 2026

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|       |                                                         |
|-------|---------------------------------------------------------|
| TCARI | Transformed Chlorophyll Absorption in Reflectance Index |
| OSAVI | Optimized Soil Adjusted Vegetation Index                |
| CCCI  | Canopy Chlorophyll Content Index                        |
| SI    | signal intensity                                        |
| CV    | coefficient of variation                                |
| S     | sensitivity                                             |

## 1. Introduction

Persimmon (*Diospyros kaki* Thunb.) is the most widely cultivated species of the genus *Diospyros*, within the Ebenaceae family. Although botanically classified as a subtropical species, it is also well adapted to temperate climates, which has allowed its successful establishment in the Mediterranean basin (George et al., 1997). China currently leads world production, whereas Spain ranks second and, together with Italy, is one of the main producing and exporting countries in the European Union (FAOSTAT, 2026). Over the last two decades, its commercial importance in Spain has increased considerably, particularly in the Valencia and Murcia regions, where persimmon orchards have gradually replaced traditional *Citrus* plantations (Buesa et al., 2013; Badal et al., 2013; Intrigliolo et al., 2018).

Persimmon expansion has occurred under increasingly restrictive environmental conditions (Buesa et al., 2013), such as in semi-arid Mediterranean regions, where fruit production relies heavily on irrigation to sustain tree productivity and fruit quality (Ferreles and Soriano, 2007; Fernández-García et al., 2020). These regions are characterised by high evaporative demand, irregular rainfall patterns and recurrent summer droughts, which are expected to intensify in the current context of climate change (IPCC, 2023). Moreover, limited water availability and increased salinity (i.e. poor irrigation water quality) can constrain persimmon performance (Parra et al., 2022). Consequently, improving irrigation water use efficiency (WUE) and selecting appropriate plant material have become key challenges for sustainable persimmon production (Visconti et al., 2017; Gil-Muñoz et al., 2020).

Despite ongoing breeding efforts to develop new varieties, only *D. kaki*, *D. lotus*, and *D. virginiana* are currently well adapted to temperate climates (Porras-Jorge et al., 2025). Whilst *D. kaki* is cultivated for fruit production, *D. lotus* and *D. virginiana* are mainly used as rootstocks. In Spain, the cultivar ‘Rojo Brillante’ of *D. kaki*, likely originated from a local mutation in the Valencian region, has become the dominant commercial variety and was awarded the Protected Designation of Origin “Kaki Ribera del Xúquer” in 1998, officially recognised by the European Union (The European Commission, 2013).

Rootstock choice plays a key role in regulating tree vigour, root system architecture, nutrient uptake and hydraulic behaviour, ultimately determining plant performance under conditions of soil water deficit (Barrios-Masías et al., 2015). *D. lotus* and *D. virginiana* exhibit different physiological characteristics. *D. lotus* has been reported to have limited soil exploration capacity and greater sensitivity to chloride toxicity (Parra et al., 2022), making it more vulnerable under saline conditions. In contrast, *D. virginiana* generally develops a more extensive root system and displays improved tolerance to adverse edaphic environments (Visconti et al., 2017; Gil-Muñoz et al., 2020).

An accurate assessment of plant water status is essential for optimising irrigation scheduling and maximising water productivity in fruit crops. Midday stem water potential ( $\Psi_{\text{stem}}$ ) is widely regarded as one of the most reliable indicators of tree water status, as it integrates soil water availability and atmospheric demand (Jones, 2007; Naor, 2000). Nevertheless, pressure chamber measurements are destructive, labour-intensive and discontinuous, which limits their use for real-time irrigation management.

Recent advances in plant-based sensing technologies offer new opportunities to overcome these limitations. Among these, trunk microtensiometers enable continuous, in-situ monitoring of water potential in woody tissues (trunk water potential,  $\Psi_{\text{trunk}}$ ), providing measurements closely aligned with traditional pressure chambers (Blanco Kalcsits,

2021; Pagay, 2022; Lakso et al., 2022; Conesa et al., 2023). Likewise, sap flow sensors using the stem heat balance (SHB) method allow for continuous estimation of transpiration dynamics, which contributes to a better understanding of plant hydraulic functioning under field conditions (Steinberg et al., 1990; Fernández et al., 2008; Steppe et al., 2015; Navarro et al., 2020). Integrating these continuous measurements with conventional discrete assessments improves our ability to unravel stomatal regulation and hydraulic responses to drought.

Although on-ground indicators provide continuous information on plant water status, their ability to represent the total area of the orchards is limited, as they are highly sensitive to spatial variability (Cohen et al., 2005) which includes (i) physicochemical soil properties (texture, depth, organic matter, etc.), (ii) plant morphology (canopy size and tree architecture), (iii) soil topography, (iv) climatic conditions (e.g. wind speed), and (v) soil and plant health (diseases and pathogens), among others (Ramírez-Cuesta et al., 2022).

Many of these limitations can be overcome using remote sensing technologies that employ thermal and multispectral (visible-near infrared, VIS-NIR) sensors mounted on unmanned aerial vehicles (UAVs) (Parra-López et al., 2025). Thermal imagery uses canopy temperature ( $T_c$ ) and the derived crop water stress index (CWSI, González-Dugo et al., 2014). Meanwhile, multispectral VIS-NIR images have been widely used to monitor physiological status of trees (i.e. vegetative growth and plant water status based on tree vigour). In this sense, the normalized difference vegetation index (NDVI, Rouse et al., 1974) is the most widely used vegetation index due to its easy computation. However, it can be affected by soil background and atmospheric conditions, particularly in orchards with partial canopy cover. For this reason, other soil-adjusted indices have been developed, such as the Optimized Soil Adjusted Vegetation Index (OSAVI; Rondeaux et al., 1996), that minimises soil reflectance effects. In addition, indices derived from the red-edge spectral region, such as the Normalized Difference Red-Edge Index (NDRE; Haboudane et al., 2002, 2004), the Canopy Chlorophyll Content Index (CCCI; Cammarano et al., 2011) and the Transformed Chlorophyll Absorption in Reflectance Index (TCARI, Haboudane et al., 2002, 2004), provide improved sensitivity to variations in canopy chlorophyll content and plant physiological activity whilst minimizing soil background effects.

Fruit tree species may adopt different water regulation strategies depending on the regulation of stomatal conductance at leaf level (Sperry et al., 1988; Flexas et al., 2004;). Trees exhibiting isohydricity tend to regulate water potential within a narrow range, thereby reducing the risk of damaging xylem cavitation caused by excessive tension in the hydraulic system of the trees (Sperry et al., 1988; Romero-Trigueros et al., 2021). In contrast, trees with an anisohydric behaviour allow their water potential to decrease during drought. This strategy enables trees to keep their stomata open and maintain carbon assimilation rates, but at a higher risk of hydraulic failure (Sperry et al., 1988; Losciale et al., 2023). In this sense, the characterisation of these hydraulic strategies using ground-based (temporal and continuous) and remote sensing indicators of plant water status in persimmon rootstocks remains poorly addressed, despite its particular relevance in semi-arid Mediterranean regions facing progressive limitations on irrigation water and declining water quality.

For these reasons, the objectives of this study were: a) to assess the physiological responses to water deficit of persimmon cv. Rojo Brillante trees, grafted onto *D. lotus* and *D. virginiana*, by assessing soil-plant water relationships during irrigation withholding to characterise their drought response strategies, and b) to assess the feasibility of new trunk microtensiometers (MTs) and SHB sap flow sensors as practical tools for precision irrigation management in persimmon trees under semi-arid Mediterranean conditions.

2. Material and methods

2.1. Experimental site and plant material

The experiment was carried out during the summer of 2025 in a 1-ha persimmon (*Diospyros kaki* Thunb.) orchard located at the CEBAS-CSIC experimental field station in Murcia (SE, Spain, 38° 06' 35" N, 1° 05' 14" W). The cultivar used was 'Rojo Brillante', which produces only female flowers and is therefore incapable of pollination (Buesa et al., 2013). The 10-year-old trees were grafted onto either *D. lotus* or *D. virginiana*, with a spacing of 3 m × 5 m in both cases.

The soil, which had a silty-clay-loam texture, was very stony, with a bulk density of 1.57 g cm<sup>-3</sup> and a low organic matter content (0.5%). The mean values of soil water content (θ<sub>v</sub>) at field capacity (FC) and permanent wilting point (WP) were 0.27 and 0.15 m<sup>3</sup> m<sup>-3</sup> respectively. The irrigation water, supplied by the distribution network of the Santomera Irrigation Community "Azarbe del Merancho" (Murcia, Spain), had an electrical conductivity (EC<sub>25</sub> °C) ranging from 0.8 to 2.5 dS m<sup>-1</sup> and a pH of 8.2, indicating slightly saline conditions (Parra et al., 2022) (Table 1).

Environmental variables, such as temperature (T), relative humidity (RH) and rainfall, amongst others, were recorded using an automatic weather station located near (≈ 300 m) the experimental plot. Reference evapotranspiration (ET<sub>0</sub>) was calculated using the FAO 56 Penman-Monteith equation (Allen et al., 1998). Vapour pressure deficit (VPD) was obtained from the RH and T values.

Fertilisers were applied to both rootstocks and applied with irrigation through the drip irrigation system (Vera and de la Peña, 1994) at a rate of 62–31–62 kg ha<sup>-1</sup> year<sup>-1</sup> of N, P<sub>2</sub>O<sub>5</sub> and K<sub>2</sub>O, respectively.

The technical staff at the CEBAS-CSIC experimental station carried out phytosanitary treatments, particularly against the Mediterranean fruit fly (*Ceratitis capitata* sp.), as well as other standard cultivation practices, such as winter pruning (during dormancy) and weed control (tilled), following local management guidelines.

2.2. Irrigation treatments and experimental design

From the beginning of the growing season (mid-March), all trees were irrigated to satisfy crop evapotranspiration requirements (ET<sub>c</sub> = 100%). ET<sub>c</sub> was estimated as the product of crop reference evapotranspiration (ET<sub>0</sub>) and crop coefficient (K<sub>c</sub>). In particular, ET<sub>0</sub> was calculated daily according to Allen et al., 1998, and K<sub>c</sub> values were obtained from previous studies by Intrigliolo et al., 2018. Irrigation was applied daily during night-time and the volume applied was recorded using in-line water meters.

Starting 17th July (day of the year, DOY, 198), two irrigation treatments were established for each rootstock: (i) Control treatment (T<sub>CTL</sub>), irrigated to 100% ET<sub>c</sub> throughout the experimental period; and (ii) Deficit irrigation treatment (T<sub>DI</sub>), in which irrigation was suspended until midday stem water potential (Ψ<sub>stem</sub>) reached −1.6 MPa (Badal et al., 2013), which corresponded to a severe water deficit. Subsequently, soil moisture content was restored to field capacity (FC), and irrigation continued as in the T<sub>CTL</sub> treatment.

The irrigation withholding protocol was designed to compare drought response dynamics between rootstocks at the same plant water status threshold rather than a fixed drought period. Consequently, the duration of the stress period differed between rootstocks, lasting: 22

days in *D. lotus* and 34 days in *D. virginiana*, respectively.

Within each rootstock, irrigation treatments were arranged in a completely randomised experimental design with four replicates. Each replicate consisted of a plot of three rows of four trees each (a total of 48 individual trees were included). Measurements were taken on the central trees of the middle row, with the surrounding trees serving as buffers trees.

2.3. Ground-based water status indicators

2.3.1. Soil measurements

Soil water status was monitored by measuring the volumetric soil water content (Θ<sub>v</sub>) using *Time Domain Reflectrometer* (TDR) soil moisture sensors (Acclima TDR-310H, Acclima Inc., USA), located next to the first water emitter towards the tree trunk on one representative tree per replicate (n = 4 per rootstock and irrigation treatment). TDR sensors were installed horizontally at depths of 0.20, 0.40 and 0.60 m (belonging to the maximum root density area, Parra et al., 2022), and connected to a radio transmission unit (RTU), which formed part of a SCADA system (addVANTAGE Pro 6.6, ADCON Telemetry, Vienna, Australia) that recorded Θ<sub>v</sub> data every 15 min.

2.3.2. Plant measurements

Physiological plant measurements were carried out using both intermittent (midday leaf (Ψ<sub>leaf</sub>) and stem (Ψ<sub>stem</sub>) water potential, and leaf gas exchange) and continuous (trunk water potential (Ψ<sub>trunk</sub>) and sap flow, SF) methods. Specifically, intermittent plant measurements were taken from 180 to 242 DOY with weekly frequency, increasing during the irrigation withholding period to every 2–3 days.

Temporal:

The Ψ<sub>leaf</sub> and Ψ<sub>stem</sub> water potentials were measured at midday (around 12:00 h GTM+2 solar time) using a pressure chamber (model 3000; Soil Moisture Equipment. Corp., Santa Barbara, CA, USA). One leaf per tree was selected from each replicate (n = 4 per rootstock and treatment). Measurements of Ψ<sub>leaf</sub> were taken on sunny freely transpiring leaves, whilst for Ψ<sub>stem</sub>, leaves were located on the shaded side of the tree, close to the tree trunk, and covered with aluminium ZIP bags for at least 2 h before the measurements (McCutchan and Shackel, 1992).

Net photosynthesis (P<sub>n</sub>), stomatal conductance (g<sub>s</sub>) and transpiration rate (E) were measured on one mature sunny leaf per replicate (n = 4 per treatment and rootstock) using a portable gas exchange system (LI-COR, LI-6400, Lincoln. NE, USA). Measurements were taken at around 11:00 h solar time, fixing ambient conditions of photosynthetic photon flux density (≈ 1200 μmol mol<sup>-1</sup>) and CO<sub>2</sub> concentration (≈ 400 μmol mol<sup>-1</sup>). From this, transpiration water use efficiency (WUE<sub>T</sub>) was calculated as the ratio of P<sub>n</sub> and E (Medrano et al., 2002).

Continuous:

Trunk water potential (Ψ<sub>trunk</sub>) was monitored using 7 mm trunk microtensiometers (MTs) (FloraPulse, Davis, CA, USA), installed on the shaded north-facing side of one tree per replicate (n = 4 per treatment and rootstock) (Fig. 1A). The MT probes were directly embedded into one of the main branches of the selected trees following the manufacturer's guidelines (Pagay et al., 2014; Lakso et al., 2022). The sensors were connected to the same RTU used for θ<sub>v</sub> measurements.

To estimate plant transpiration, sap flow (SF) rates were measured

Table 1  
Chemical composition of irrigation water.

|                          |           | mg •L <sup>-1</sup>           |              |                  |              |    |           |
|--------------------------|-----------|-------------------------------|--------------|------------------|--------------|----|-----------|
| pH                       | 7.6 ± 0.4 | Cl <sup>-</sup>               | 351 ± 29.3   | Ca <sup>2+</sup> | 179.9 ± 31.6 | B  | 0.4 ± 0.1 |
| CE (dS•m <sup>-1</sup> ) | 2.1 ± 0.1 | NO <sup>3-</sup>              | 20.7 ± 5.8   | Mg <sup>2+</sup> | 107.5 ± 16.3 | Fe | <0.01     |
|                          |           | SO <sub>4</sub> <sup>2-</sup> | 623.4 ± 79.2 | Na <sup>+</sup>  | 287.7 ± 51.2 | Mn | 0.7 ± 0.0 |
|                          |           | PO <sub>4</sub> <sup>2-</sup> | 1.12 ± 0.18  | K <sup>+</sup>   | 16.6 ± 1.0   | Cu | <0.01     |

Values are the average of monthly samples from March to October 2025.

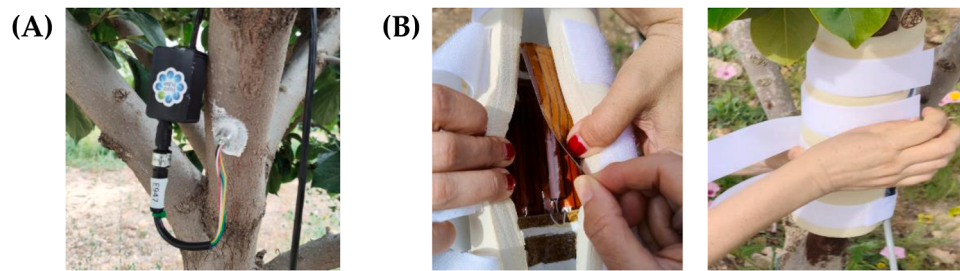


Fig. 1. Detail of the MTs probes (A), and SHB sap flow sensors (B) installed in persimmon trees.

using the stem heat balance (SHB) technique (Baker and van Bavel, 1987). The SHB sap flow sensors used were SGB50, designed to operate in a stem diameter range of 70 - 95 mm (Dynamax Inc. Houston, TX, USA). The sensors were installed on a main branch of the same trees used for  $\Psi_{\text{trunk}}$ , on the shaded north-facing side of each replicate ( $n = 4$  per treatment and rootstock) (Fig. 1B), according to the manufacturer's instructions (Dynagage sap flow sensor manual, Dynamax Inc, 2007). Data from the sensors were collected at 30 s intervals and recorded at 15 min intervals using a datalogger (CR1000X, Campbell Scientific Inc. Logan, UT, USA). SF was calculated from the hourly raw data using the equations of Baker and van Bavel, 1987 with the datalogger support software PC400 (Campbell Scientific Inc., Logan, UT, USA). Afterwards, SF data were normalized to account for differences in branch architecture among trees and rootstocks. This normalization assumed a uniform distribution of SF relative to branch perimeter and it was calculated as the ratio between the perimeter of the monitored main branch and the mean integrated perimeter of all main branches of each selected tree.

#### 2.4. Remote sensing indicators

The remote sensing indicators were collected during an aerial campaign conducted by Centro Tecnológico de la Construcción (CTCON <https://ctcon-rm.com/es/>) on DOY 218, coinciding with the period of maximum water stress in the  $T_{\text{DI}}$  treatments. The images were obtained using an unmanned aerial vehicle (UAV) platform (DJI Matrice 200) equipped with a dual payload consisting of a radiometric thermal camera (DJI Zenmuse XT2) and a multispectral camera (MicaSense), integrated through the DJI SkyPort interface. Flights were conducted around solar noon (12:00 h GTM+2) at an altitude of 120 m, ensuring high spatial resolution imagery of the canopy of the persimmon orchard.

Thermal imagery captured by the Zenmuse XT2 operating in the long-wave infrared (LWIR, 8–14  $\mu\text{m}$ ) range was used to estimate canopy temperature ( $T_c$ ). Multispectral imagery obtained in the VIS–NIR spectral regions enabled the calculation of vegetation indices related to canopy vigour and plant water status. Specifically, several indices were derived, including NDVI, NDRE, OSAVI, TCARI, RNDVI and CCCI (as reviewed by Xue and Su, 2017). In addition, a database of remote sensing indices can be found in <https://www.indexdatabase.de/>.

#### 2.5. Sensitivity analysis

The sensitivity of the different plant water stress indicators was assessed using the method proposed by Goldhamer & Fereres, 2001, as:

$$S = SI / CV$$

where  $S$  represents the sensitivity index,  $SI$  is the signal intensity, and  $CV$  corresponds to the coefficient of variation ('noise'). Signal intensity ( $SI$ ) was calculated as the ratio of the mean values of the water deficit ( $T_{\text{DI}}$ ) and the control ( $T_{\text{CTL}}$ ) treatments of each rootstock. Since  $S$  is always greater than 0, higher values indicate greater sensitivity of the indicator to water stress.

This sensitivity analysis was used as a comparative metric among indicators rather than as a standalone criterion of biological

responsiveness, since the  $S$  index integrates both treatment signal intensity and within-treatment variability (Goldhamer and Fereres, 2001). Therefore, its interpretation should be complemented with the magnitude and direction of the treatment response, statistical significance, and the physiological relevance of each indicator (Jones, 2004). All measurements were taken on the same trees throughout the experiment to avoid potential interference from sampling date, sample type or sample size in the sensitivity analysis.

#### 2.6. Statistical analysis

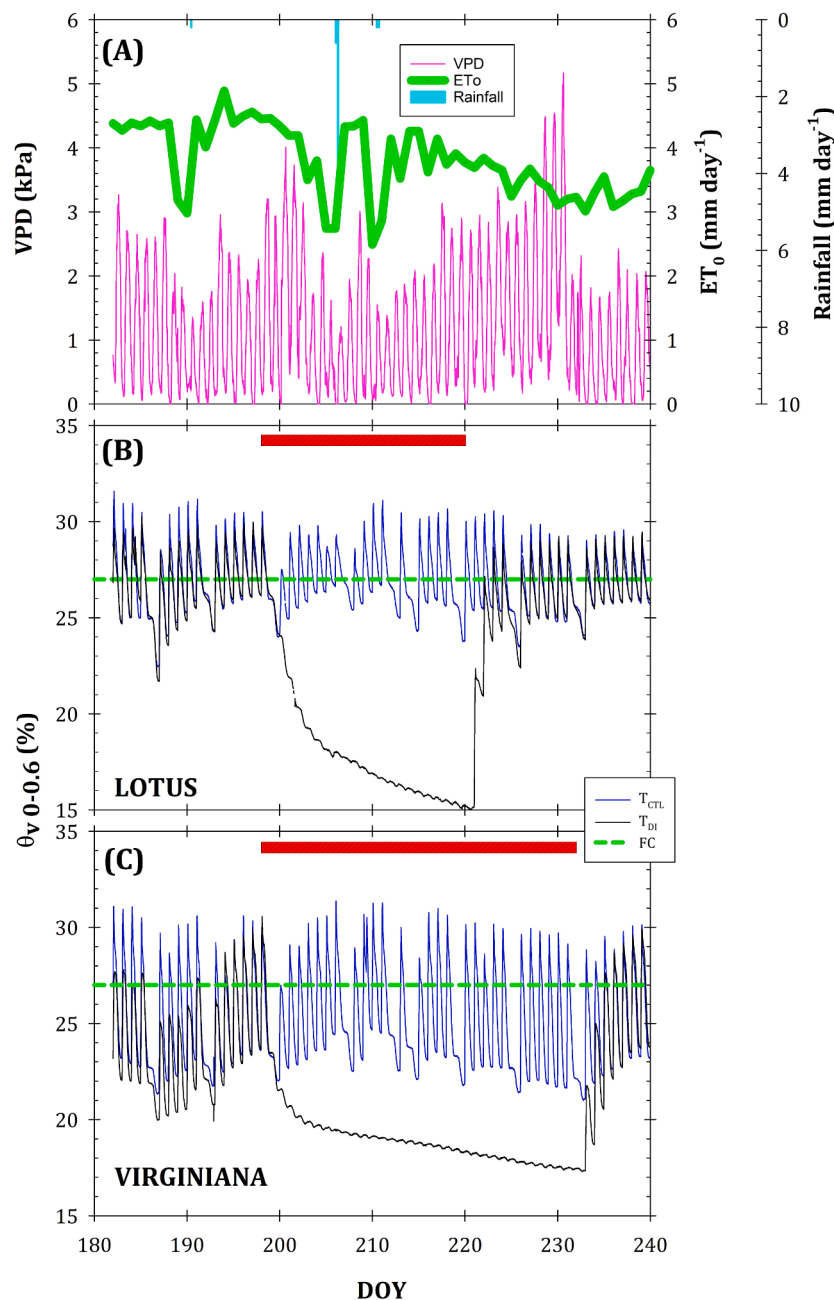
The effects of water deficit and rootstocks on measured variables were discriminated using SPSS v 9.1 (IBM, Armonk, NY, USA). Normality and homoscedasticity were first assessed. After that, a two-way ANOVA was performed to assess the effects of the main factors: treatments (T), rootstocks (R) and the interaction  $T \times R$  using Least Significant Difference (LSD) multiple range test ( $p < 0.05$ ). When the interaction was significant the effect of main factors cannot be assessed, since the effect of a factor depends on the level of the other (Moreno-Lara et al., 2026). Additionally, correlation analyses were performed to determine the relationship between treatments within each rootstock, and the coefficient of determination ( $r^2$ ) was used to assess the goodness-of-fit of the associations, whilst the mean squared error (MSE) was calculated to assess the variability among the indicators studied.

### 3. Results

#### 3.1. Environmental conditions and soil water status

Fig. 2 shows the environmental conditions and soil water dynamics during the experimental period (DOY 182–242). The average daily climatic conditions were characterised by indicators such as VPD of 2.2 kPa and  $ET_0$  of 3.8 mm day<sup>-1</sup>, resulting in a high cumulative evaporative demand of 253.4 mm. This atmospheric demand represented approximately 70% of the crop water requirements during the irrigation season, whilst rainfall was negligible (3.6 mm during the period, Fig. 2A). These conditions were accompanied by consistently high levels of solar radiation (data not shown), typical of summer climates.

Under these climatic conditions,  $\theta_v$  was largely influenced by irrigation events and plant water uptake. The irrigation applied in  $T_{\text{CTL}}$  of both rootstocks totalled 194.9 mm during the experimental period, maintaining a relatively stable  $\theta_v$ , around 25% and 28% in *D. virginiana* and *D. lotus*, respectively, with a greater daily soil water depletion in *D. virginiana* (Figs. 2B–C). In contrast, the  $T_{\text{DI}}$  treatments involved a reduction in irrigation of 37% in *D. lotus* and 57% in *D. virginiana* compared with the  $T_{\text{CTL}}$  treatment. As a result,  $\theta_v$  progressively decreased following the onset of the stress period, reaching minimum values of 15% and 18% in the  $T_{\text{DI}}$  treatments of *D. lotus* and *D. virginiana*, respectively. It should be noted that this decrease occurred more gradually and that the minimum  $\theta_v$  remained considerably higher in *D. virginiana* than in *D. lotus*. Withholding irrigation did not reduce  $\theta_v$  below the wilting point in any rootstock (Figs. 2B–C).



**Fig. 2.** Seasonal evolution of (A) VPD (pink line, kPa), ET<sub>0</sub> (green dotted line, mm day<sup>-1</sup>), and rainfall (cyan vertical bar, mm); and (B) average  $\theta_v$  (%) in the soil profile 0–0.6 m for *D. lotus* and (C) *D. virginiana* for T<sub>CTL</sub> — and T<sub>DI</sub> — treatments. In Figs. B–C, the green dashed line indicates the field capacity (FC) value. The horizontal red bar indicates the stress period of each rootstock. The values are the average of four sensors at 0.2, 0.4 and 0.6 m for each treatment and rootstock. DOY: Day of the year.

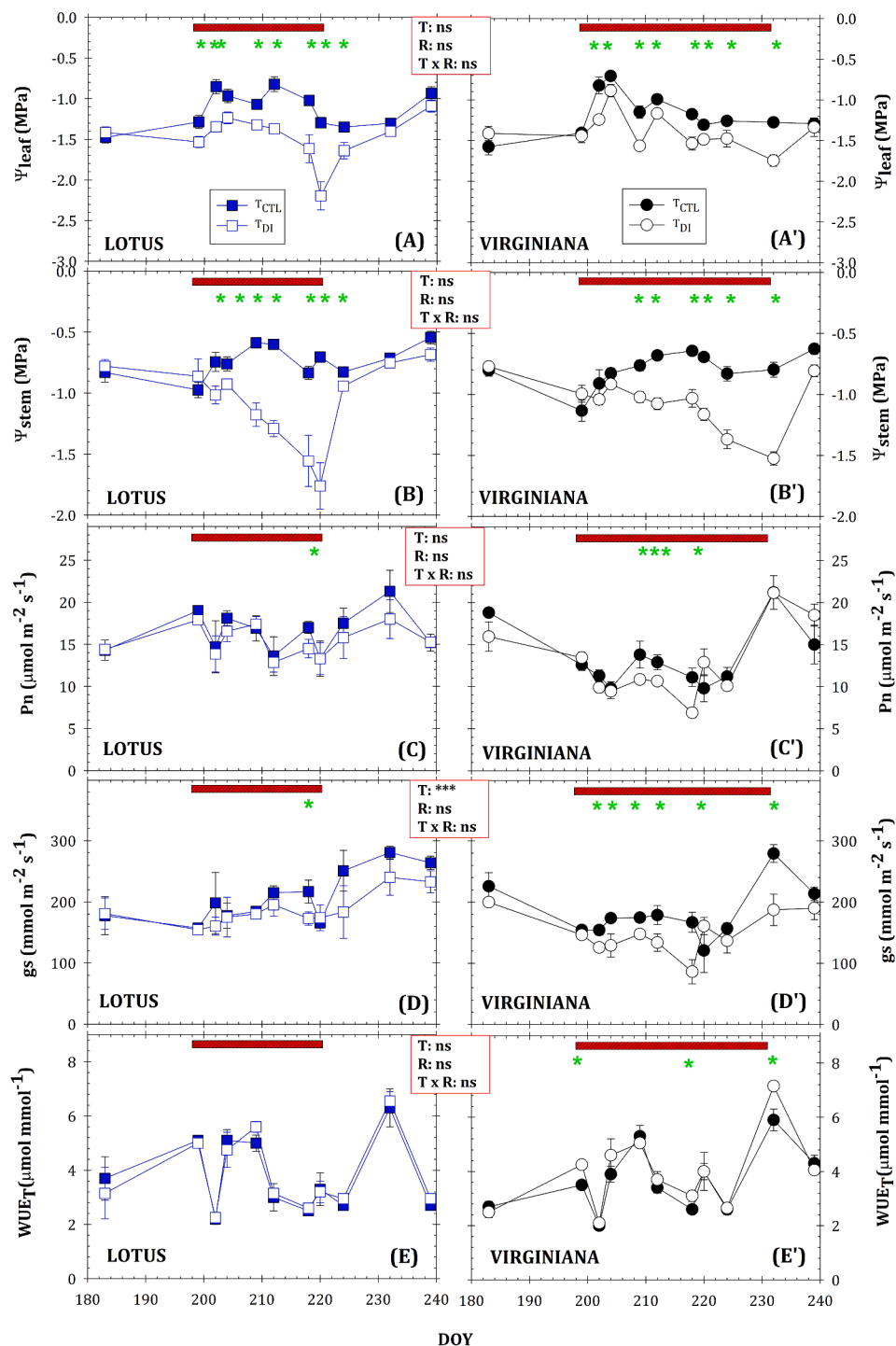
### 3.2. Ground-based plant water relations

Both  $\Psi_{\text{leaf}}$  and  $\Psi_{\text{stem}}$  decreased progressively during the irrigation withholding period, with a more pronounced reduction in *D. lotus* (Figs. 3A–B). Under well-irrigated conditions (T<sub>CTL</sub>),  $\Psi_{\text{stem}}$  values remained around  $-0.80$  MPa for both rootstock (Figs. 3B–B'), whereas the severe stress imposed by T<sub>DI</sub> conditions resulted in minimum  $\Psi_{\text{stem}}$  values of  $-1.76$  MPa (DOY 220) and  $-1.58$  MPa (DOY 232) for *D. lotus* and *D. virginiana*, respectively (Figs. 3B–B'). Overall, *D. lotus* showed greater sensitivity to water deficit, whilst *D. virginiana* maintained a comparatively better plant water status, with  $\Psi_{\text{stem}}$  values generally above  $-1.5$  MPa during the water withholding period (Fig. 3B'). A similar trend was observed for  $\Psi_{\text{leaf}}$ , although the differences between

treatments were less consistent (Figs. 3A–A'), indicating greater variability at the leaf level compared with  $\Psi_{\text{stem}}$  measurements. In this regard,  $\Psi_{\text{leaf}}$  reached values close to  $-2.2$  MPa under stress in *D. lotus* (Fig. 3A), whereas in *D. virginiana* values generally ranged between  $-1.0$  and  $-1.7$  MPa (Fig. 3A').

The parameters of leaf gas exchange showed clear rootstock-dependent physiological responses. In *D. lotus*,  $P_n$  remained relatively stable throughout the experimental period, with only minor differences between irrigation treatments (Fig. 3C), showing a 17% reduction in T<sub>DI</sub> compared to T<sub>CTL</sub> values. In contrast, *D. virginiana* exhibited a more pronounced decrease in  $P_n$  during the stress period, with reductions of approximately 31% in T<sub>DI</sub> compared to T<sub>CTL</sub> values (Fig. 3C').

The most sensitive of the gas exchange parameters to water stress



**Fig. 3.** Seasonal trend of (A)  $\Psi_{\text{leaf}}$  (MPa), (B)  $\Psi_{\text{stem}}$  (MPa), (C)  $P_n$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), (D)  $g_s$  ( $\text{mmol m}^{-2} \text{s}^{-1}$ ), and (E)  $\text{WUE}_T$  ( $\mu\text{mol mmol}^{-1}$ ), of *D. lotus*, and *D. virginiana* (marked with ') for  $T_{\text{CTL}}$  (filled symbols) and  $T_{\text{DI}}$  (open symbols) treatments. The horizontal red bar indicates the stress period for each rootstock. Values are the average of four leaves  $\pm$  SE. Asterisk indicates significant differences between treatments at  $p < 0.05$ . For each indicator, the effect of a two-way ANOVA is showed: Treatment (T), Rootstock (R) and  $T \times R$  interaction (\*\*\*:  $p < 0.001$ , ns: not significant). DOY: Day of the year.

was the  $g_s$ , as shown by the two-way ANOVA (Fig. 3D-D'). In *D. lotus*,  $g_s$  showed moderate decreases under water deficit, falling from approximately 180–220 to 150–180  $\text{mmol m}^{-2} \text{s}^{-1}$  ( $\approx 15$ –25% reduction). In contrast, *D. virginiana* showed a stronger and more consistent decrease, particularly during maximum stress conditions, with  $g_s$  decreasing from approximately 180–200 to 100–140  $\text{mmol m}^{-2} \text{s}^{-1}$  ( $\approx 35$ –50% reduction). By the end of the water deficit period, *D. lotus* and *D. virginiana* had already reached similar reductions in  $g_s$  and  $P_n$  (compared to their  $T_{\text{CTL}}$ ),

comparable to those observed at the end of their own deficit period, which occurred 12 days later in *D. virginiana*. Notably, during this interval,  $g_s$  and  $P_n$  in *D. virginiana* remained high and only began to decline once VPD decreased following the resumption of irrigation (Fig. 3).

Likewise,  $\text{WUE}_T$  showed no clear or consistent differences between the treatments or rootstocks, with values generally ranging between 3 and 6  $\mu\text{mol mmol}^{-1}$ , reflecting the combined variability of  $P_n$  and transpiration (Fig. 3E-E').

The temporal dynamics of  $\Psi_{\text{trunk}}$ , assessed with novel MTs, clearly reflected the progression of soil water depletion and clearly discriminated between treatments earlier and more consistently than the previous discrete measurements (Fig. 3).

Under well-irrigated conditions ( $T_{\text{CTL}}$ ),  $\Psi_{\text{trunk}}$  remained relatively stable in both rootstocks, with values generally ranging between  $-0.4$  and  $-0.8$  MPa (Figs. 4A-A'). In contrast, irrigation withholding induced a pronounced decline in the  $\Psi_{\text{trunk}}$  values of the  $T_{\text{DI}}$  treatment, particularly in *D. lotus*, where values decreased sharply during the stress period and reached minimum values close to  $-2.2$  MPa (Fig. 4A). This decline in *D. virginiana* was less pronounced, with  $\Psi_{\text{trunk}}$  stressed values above  $-1.2$  MPa (Fig. 4A'). A mean gradient between  $\Psi_{\text{trunk}}$  values of  $T_{\text{CTL}}$  and  $T_{\text{DI}}$  over the entire study period was  $\approx 0.25$  MPa for *D. lotus* and  $\approx 0.50$  MPa for *D. virginiana* (Fig. 4A-A'). Additionally, when irrigation was resumed in both  $T_{\text{DI}}$  treatments,  $\Psi_{\text{trunk}}$  recovery differed between rootstocks; in *D. lotus*, the values failed to fully recover to control levels (Fig. 4A).

Sap flow (SF) values showed different patterns between treatments (T) and rootstocks (R), even though their interaction was not significant (Figs. 4B-B'). Persimmon trees from  $T_{\text{CTL}}$  showed consistently higher SF rates (approximately  $30\text{--}70$  L tree $^{-1}$  day $^{-1}$ ) in *D. virginiana* compared to those observed in *D. lotus* (approximately  $15\text{--}35$  L tree $^{-1}$  day $^{-1}$ ), suggesting a higher transpiration capacity of the former rootstock. In  $T_{\text{DI}}$ , SF tended to decrease in both rootstocks, although the magnitude and pattern of the decrease was different. In *D. lotus*, SF rates remained low throughout the experimental period, with only slight decreases under stress conditions (Fig. 4B). In contrast, *D. virginiana* showed a more pronounced decrease in SF values during the stress period, averaging a reduction of 54% in the  $T_{\text{DI}}$  persimmon trees compared to the  $T_{\text{CTL}}$  ones (Fig. 4B').

A strong linear relationship was found between  $\Psi_{\text{stem}}$  vs.  $\Psi_{\text{trunk}}$  (Fig. 5A). This relationship was particularly high in *D. lotus* ( $r^2 = 0.84$ ,  $p < 0.001$ ), suggesting a close relationship between both indicators. In *D. virginiana*, the relationship was also significant, but slightly weaker

than in *D. lotus* ( $r^2 = 0.63$ ,  $p < 0.001$ )

In contrast, the relationship between  $\Psi_{\text{stem}}$  vs. SF was more variable (Fig. 5B). Although significant correlations were observed in both rootstocks, the strength of the relationship was lower compared to that of  $\Psi_{\text{stem}}$  vs.  $\Psi_{\text{trunk}}$ , with  $r^2$  values of 0.41 and 0.30 for *D. virginiana* and *D. lotus*, respectively. More importantly, SF values decreased as  $\Psi_{\text{stem}}$  declined, reflecting reduced transpiration under water deficit conditions, although the greater dispersion in data likely indicated that SF was influenced not only by plant water status but also by other factors such as canopy size:  $1.52$  m $^2$  (*D. lotus*) vs.  $3.28$  m $^2$  (*D. virginiana*), as measured using UAV flight.

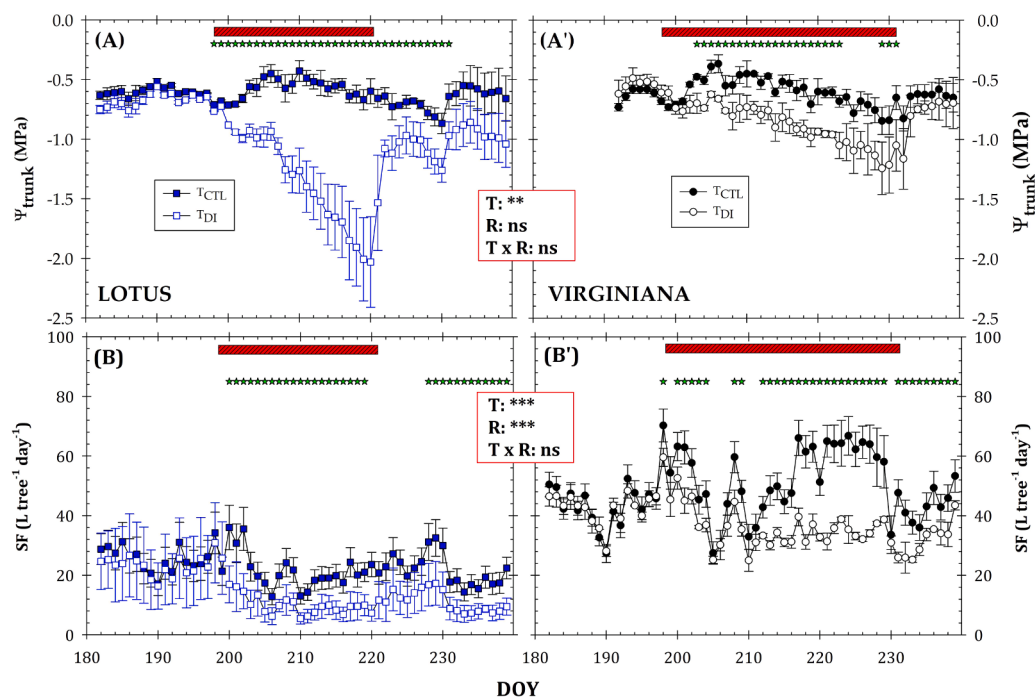
Furthermore, a significant negative relationship was observed between  $\Psi_{\text{trunk}}$  vs. SF in both rootstocks (Fig. 6). SF decreased as  $\Psi_{\text{trunk}}$  became more negative, reflecting the progressive reduction in transpiration under increasing water deficit.

The strength of this relationship varied between rootstocks. In *D. lotus*, a moderate correlation was found ( $r^2 = 0.51$ ,  $p < 0.001$ ), with a gradual decline in SF as  $\Psi_{\text{trunk}}$  decreased. In contrast, *D. virginiana* showed a slightly weaker relationship ( $r^2 = 0.44$ ,  $p < 0.001$ ), but with a steeper slope, indicating a stronger reduction in SF (transpiration) per unit decrease of  $\Psi_{\text{trunk}}$ .

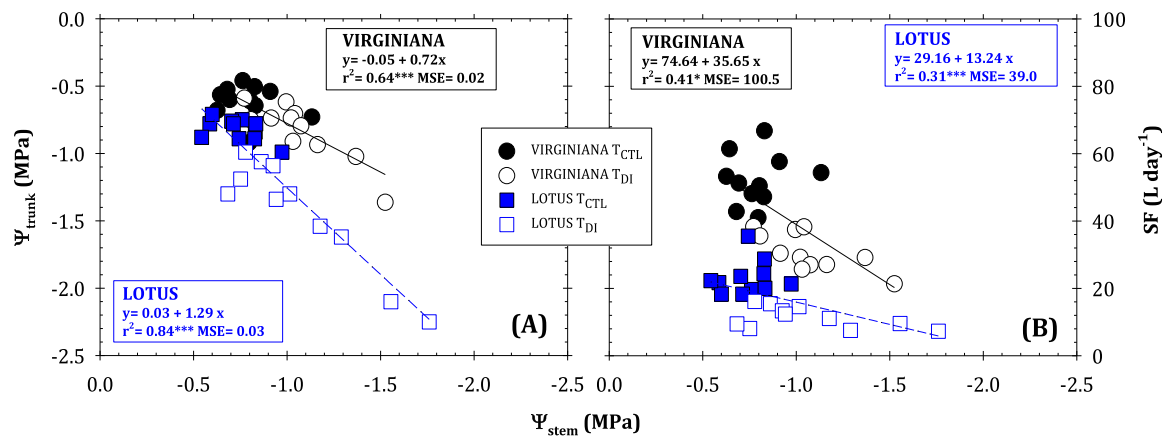
### 3.3. Remote sensing plant indicators

Canopy temperature ( $T_c$ ) was the most responsive UAV-derived indicator assessed (Fig. 7A), as it was significantly affected by both treatment and rootstock factors ( $p < 0.001$ ) and showed a consistent increase under  $T_{\text{DI}}$  conditions for both rootstocks. In *D. lotus*, the mean  $T_c$  increased from  $31.2$  °C ( $T_{\text{CTL}}$ ) to  $34.1$  °C ( $T_{\text{DI}}$ ), whilst in *D. virginiana* this increase was lower (Fig. 7A), from  $29.3$  ( $T_{\text{CTL}}$ ) to  $30.9$  ( $T_{\text{DI}}$ ).

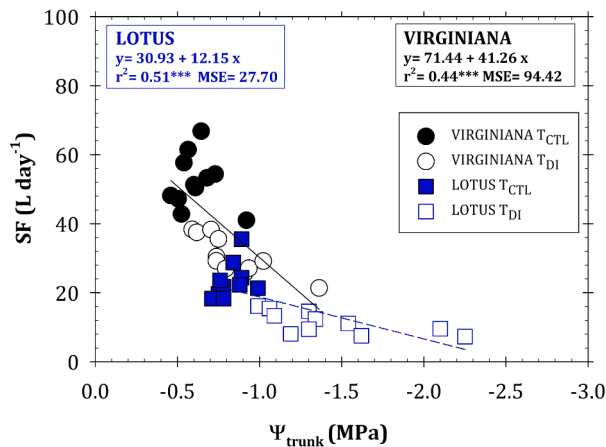
Spectral vegetation indices showed little sensitivity to the irrigation treatment but a predominantly driven rootstock effect (Figs. 7B-F). NDVI was significantly affected by rootstock ( $p < 0.001$ ), whilst no significant differences were detected between irrigation treatments.



**Fig. 4.** Seasonal trend of (A)  $\Psi_{\text{trunk}}$  at midday (MPa) and (B) daily SF (L tree $^{-1}$  day $^{-1}$ ) of *D. lotus*, and *D. virginiana* (indicated with ') for  $T_{\text{CTL}}$  (filled symbols) and  $T_{\text{DI}}$  (open symbols) treatments. The horizontal red bar indicates the stress period of each rootstock. The values are the average of four MTs and four SHB sap flow sensors  $\pm$  SE. Asterisks denote significant differences between treatments at  $p < 0.05$ . Asterisks denote significant differences between treatments at 95% of confidential level. For each indicator, the effect of a two-way ANOVA is showed: Treatment (T), Rootstock (R) and  $T \times R$  interaction (\*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ , ns: not significant). DOY: Day of the year.



**Fig. 5.** Linear relationships between  $\Psi_{\text{stem}}$  vs.  $\Psi_{\text{trunk}}$  (A) and  $\Psi_{\text{stem}}$  vs. SF (B) in *D. lotus* and *D. virginiana* for T<sub>CTL</sub> and T<sub>DI</sub> treatments.  $\Psi_{\text{trunk}}$  and SF data were recorded at the same time as the  $\Psi_{\text{stem}}$  measurements. The values are the average of four leaves and four MTs and SHB sap flow sensors per treatment. \*:  $p < 0.05$ , \*\*\*:  $p < 0.001$ , MSE: mean squared error.



**Fig. 6.** Linear relationship between  $\Psi_{\text{trunk}}$  vs. SF in *D. lotus* and *D. virginiana* for T<sub>CTL</sub> and T<sub>DI</sub> treatments. The values are the average of four leaves and four MTs and SHB sap flow sensors per treatment during the season. \*\*\*:  $p < 0.001$ , MSE: mean squared error.

According to this, significantly higher values were observed for *D. virginiana* in T<sub>CTL</sub> (0.83) compared to T<sub>DI</sub> (0.80), whereas *D. lotus* showed no significant effect of the irrigation treatment (Fig. 7B).

Similarly, NDRE was significantly influenced by rootstock ( $p < 0.001$ ), with no differences in mean values of *D. lotus*, which ranged from 0.36 (T<sub>CTL</sub>) to 0.37 (T<sub>DI</sub>), and a significant treatment effect for *D. virginiana* (T<sub>CTL</sub> = 0.50 vs. T<sub>DI</sub> = 0.47) (Fig. 7C).

OSAVI followed the same trend as NDVI and NDRE, showing significantly higher values for *D. virginiana* than for *D. lotus*, but with no significant response to the irrigation regime applied (Fig. 7E).

For its part, TCARI showed a moderate but significant effect of irrigation treatment ( $p < 0.05$ ) (Fig. 7D). In *D. lotus*, TCARI increased slightly from 0.16 (T<sub>CTL</sub>) to 0.17 (T<sub>DI</sub>), whereas in *D. virginiana* it ranged from 0.11 (T<sub>CTL</sub>) to 0.13 (T<sub>DI</sub>).

Interestingly, CCCI was significantly affected by the treatment, rootstock as well as by the interaction R x T ( $p < 0.05$ ) (Fig. 7F). Mean values were higher in *D. virginiana* (0.61 T<sub>CTL</sub> vs. 0.59 T<sub>DI</sub>) than in *D. lotus* (0.48 T<sub>CTL</sub> vs. 0.52 T<sub>DI</sub>), with a significant increase in the deficit irrigation treatment (T<sub>DI</sub>).

### 3.4. Sensitivity analysis

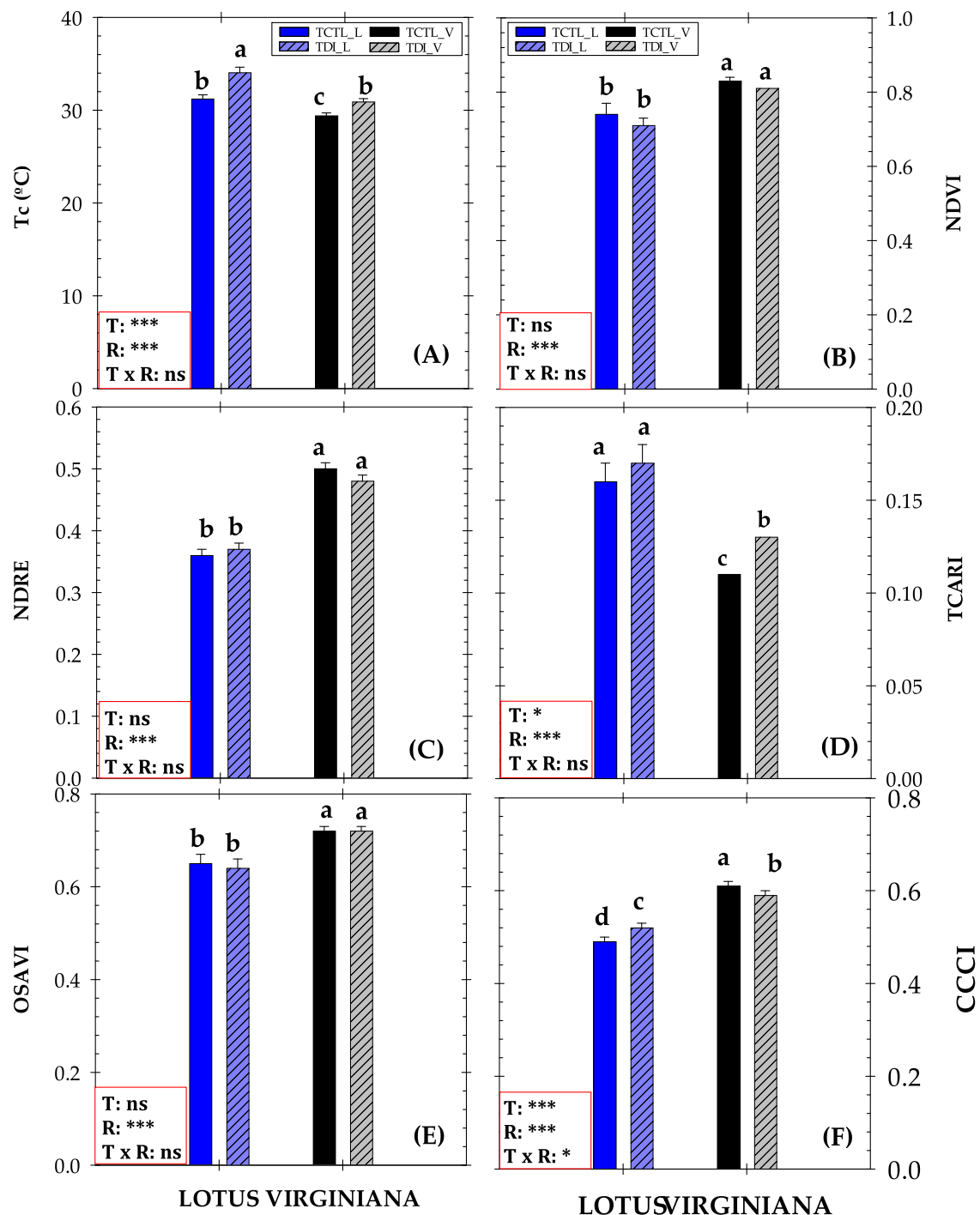
Overall, ground-based indicators were more sensitive for *D. lotus* than for *D. virginiana*, suggesting a stronger physiological response to water deficit in this rootstock. Among these indicators,  $\Psi_{\text{trunk}}$  showed the highest sensitivity (S) to water deficit in both rootstocks (Table 2) following by  $\Psi_{\text{stem}}$  confirming the strong responsiveness of both continuous and discrete water potential measurements to soil water depletion. Meanwhile,  $\Psi_{\text{leaf}}$  showed a more moderate responsiveness that depended on environmental conditions. Nevertheless, S values should be interpreted with caution, since the S index integrates both treatment response and its variability. In contrast, gas exchange variables ( $P_n$  and  $g_s$ ) and sap flow (SF) measurements showed low S values, suggesting that their variability exceeded the signal triggered by water deficit, limiting their usefulness as stress indicators. WUE<sub>T</sub> showed intermediate sensitivity with relatively stable S values for both rootstocks (Table 2).

Regarding the UAV-derived variables, T<sub>c</sub> was the remote sensing indicator that most consistently reflected the water deficit imposed in this study, with high S values and relatively low variability (Table 2), supporting its practical value as a thermal indicator of short-term stress. By contrast, the multispectral indices showed a more variable response between rootstocks. NDVI exhibited the highest S value in *D. virginiana*, whereas CCCI was the most responsive spectral index in *D. lotus*. However, both NDVI and CCCI were less consistent than T<sub>c</sub> and likely more influenced by structural and vigour related-differences between rootstock than by water deficit alone.

## 4. Discussion

Our results showed that persimmon trees (*Diospyros kaki* Thunb.) exhibited rootstock-dependent hydraulic strategies, suggesting that rootstock selection plays a crucial role in determining drought-coping strategies of cv. 'Rojo Brillante'.

Under control conditions, the mean  $\theta_v$  values (Figs. 2B-C) remained close to field capacity for both rootstocks, while  $\Psi_{\text{stem}}$  values were indicative of non-limiting soil water conditions (Fig. 3B-B'), consistent with previous studies on the same cultivar (Buesa et al., 2013; Visconti et al., 2017; Parra et al., 2022). Under these conditions, a higher daily water absorption capacity was also observed in *D. virginiana*, which was more readily assimilated (Figs. 2B-C). During the imposed soil water deficit, the water withholding period led to a decrease in mean  $\theta_v$  values for both rootstocks, which was more pronounced for *D. lotus* than for *D. virginiana*, this difference being influenced by the duration of the stress period in each rootstock. Specifically, *D. lotus* reached the  $\Psi_{\text{stem}}$



**Fig. 7.** Mean values of: (A) canopy temperature (Tc, °C), (B) Normalized Difference Vegetation Index (NDVI), (C) Normalized Difference Red-Edge Index (NDRE), (D) Transformed Chlorophyll Absorption in Reflectance Index (TCARI), (E) Optimized Soil Adjusted Vegetation Index (OSAVI), and (F) Canopy Chlorophyll Content Index (CCCI), assessed by UAV flight (VIS-NIR and thermal cameras) on DOY 218. Different letters indicate significant differences between irrigation treatments (TCTL and TDL) according to LSD<sub>0.05</sub> test. Values are means + SE of 8 trees per treatment and rootstock. For each indicator, the effect of a two-way ANOVA is indicated: Treatment (T), Rootstock (R), and T × R interaction (\*:  $p < 0.05$ ; \*\*\*:  $p < 0.001$ ; ns: not significant).

threshold value of  $-1.6$  MPa, (indicating severe water deficit in persimmon trees, according to Badal et al., 2013) 22 days after irrigation was suspended, and *D. virginiana* did so after 34 days, even though both rootstocks were grown under identical soil, orchard and fertilization conditions. The longer irrigation withholding period observed in *D. virginiana* should not be only interpreted as an experimental factor, but rather as part of the biological persimmon response to drought. In this sense, the delayed attainment of the target  $\Psi_{\text{stem}}$  threshold suggests contrasting drought-response dynamics between both rootstocks and

likely reflects a greater capacity of *D. virginiana* to maintain plant water status under progressive soil water depletion (Figs. 2 and 3). Therefore, comparisons between rootstocks should consider both the physiological responses at a common  $\Psi_{\text{stem}}$  threshold, and the different rates of stress progression, as drought responses strongly depend on the temporal dynamics of plant hydraulic regulation (Tardieu and Simonneau, 1998; Martínez-Vilalta et al., 2014).

Furthermore, according to the studies reported by Visconti et al., 2017 and Gil-Muñoz et al., 2020, *D. lotus* has been described as a

**Table 2**  
Sensitivity analysis for ground-based and remote sensing plant indicators during the UAV flight of the *D. lotus* and *D. virginiana* persimmon trees.

| Ground-based indicators   | <i>D. virginiana</i> |       |       | <i>D. lotus</i> |       |       |
|---------------------------|----------------------|-------|-------|-----------------|-------|-------|
|                           | SI                   | CV    | S     | SI              | CV    | S     |
| $\Psi_{leaf}$             | 1.32                 | 8.74  | 0.15  | 2.06            | 10.1  | 0.2   |
| $\Psi_{stem}$             | 1.62                 | 6.02  | 0.27  | 2.16            | 7.59  | 0.28  |
| $P_n$                     | 0.87                 | 17.04 | 0.05  | 0.55            | 14.38 | 0.04  |
| $g_s$                     | 0.47                 | 22.51 | 0.02  | 0.33            | 10.78 | 0.03  |
| $WUE_T$                   | 1.17                 | 8.15  | 0.14  | 1.26            | 14.61 | 0.09  |
| $\Psi_{trunk}$            | 1.67                 | 3.57  | 0.47  | 2.51            | 4.02  | 0.63  |
| SF                        | 0.39                 | 18.38 | 0.02  | 0.75            | 23.44 | 0.03  |
| Remote sensing indicators | SI                   | CV    | S     | SI              | CV    | S     |
| $T_c$                     | 1.05                 | 0.05  | 20.76 | 1.09            | 0.07  | 15.82 |
| NDVI                      | 0.98                 | 0.04  | 24.73 | 0.97            | 0.16  | 6.2   |
| NDRE                      | 0.96                 | 0.07  | 13.64 | 1.02            | 0.16  | 6.3   |
| TCARI                     | 1.19                 | 0.13  | 9.32  | 1.03            | 0.17  | 6.22  |
| OSAVI                     | 0.99                 | 0.06  | 17.94 | 0.98            | 0.15  | 6.45  |
| CCCI                      | 0.98                 | 0.07  | 14.95 | 1.05            | 0.07  | 14.88 |

Values taken at 12:00 h solar time are means of four replicates (leaves/monitored trees). SI, signal intensity; CV, coefficient of variation (%); S, SI/CV (Goldhamer and Fereres, 2001)  $\Psi_{leaf}$ , leaf water potential at midday (MPa);  $\Psi_{stem}$ , midday stem water potential (MPa);  $P_n$ , net photosynthesis ( $\text{mol m}^{-2} \text{s}^{-1}$ );  $g_s$ , stomatal conductance ( $\text{mmol m}^{-2} \text{s}^{-1}$ );  $WUE_T$ , instantaneous water use efficiency ( $\mu\text{mol mmol}^{-1}$ );  $T_c$ , canopy temperature ( $^{\circ}\text{C}$ ); NDVI, normalized difference vegetation index; Normalized Difference Red-Edge Index (NDRE); Transformed Chlorophyll Absorption in Reflectance Index (TCARI); Optimized Soil Adjusted Vegetation Index (OSAVI); Canopy Chlorophyll Content Index (CCCI).

rootstock with limited soil exploration capacity, which restricts access to water stored in deeper soil layers and thus increases susceptibility to water and salinity stresses (Table 1). Conversely, *D. virginiana* typically develops a more extensive and deeper root system, supporting greater tolerance to adverse edaphic conditions such as drought and salinity. These morphological differences in the root system are consistent with the delayed ending of the stress period observed in this study in *D. virginiana*.

Our results show that the choice of rootstock strongly determines plant response to water deficit. *D. lotus* showed a rapid decline in both  $\Psi_{stem}$  and  $\Psi_{trunk}$  under irrigation withholding (Figs. 3B and 4 A). In contrast, *D. virginiana* maintained higher water potentials throughout the stress period (Figs. 3B' and 4 A'). These differences suggest contrasting hydraulic regulation strategies along the isohydric–aniso-hydric continuum (Tardieu and Simonneau, 1998; Flexas et al., 2004). In *D. lotus*, the observed sharp decline in  $\Psi_{stem}$  and  $\Psi_{trunk}$  together with the relatively stable tendency of  $P_n$  and  $g_s$  (Figs. 3C, D), is consistent with a more aniso-hydric-like response, in which stomata regulation is partially maintained despite decreasing water potentials. In contrast, *D. virginiana* showed stronger stomatal regulation, with more pronounced reductions in leaf gas exchange (Figs. 3C', D') and a more conservative hydraulic strategy, which is consistent with isohydric-like behaviour under water deficit conditions. Similar contrasting strategies have been reported in woody crops, where aniso-hydric genotypes maintain carbon assimilation under stress, while isohydric genotypes prioritize hydraulic safety (Medrano et al., 2002; Martínez-Vilalta et al., 2014; Conesa et al., 2016; Navarro et al., 2018; Romero-Trigueros et al., 2021; Losciale et al., 2023).

These findings reinforce the importance of rootstock selection in Mediterranean environments, where water scarcity is expected to intensify (IPCC, 2023; Lionello et al., 2023). In this context, the ability of *D. virginiana* to regulate water loss more effectively could offer greater resilience during prolonged drought, whereas *D. lotus*, even though it is the most widely used rootstock under Mediterranean conditions due to its higher productive potential (Parra et al., 2022; Porras-Jorge et al., 2025), has revealed to be potentially more vulnerable to water availability and salinity, especially in long-term studies.

Among the indicators of plant water status evaluated, continuous

$\Psi_{trunk}$  measurements using novel MTs proved to be the most sensitive and robust indicator of persimmon water status (Figs. 4A–A'). The strong correlation between  $\Psi_{stem}$  and  $\Psi_{trunk}$  in both rootstocks (Fig. 5) confirms that  $\Psi_{trunk}$  reliably reflects the water status of persimmons, in agreement with recent studies on pears (Blanco and Kalcits, 2021), nectarines (Conesa et al., 2023; Vera et al., 2025), apples (Lakso et al., 2022; Blanco and Kalcits, 2024), grapevines (Pagay, 2022), cotton (Christerson et al., 2024), kiwifruits (Di Biase et al., 2025) and *Citrus* tree species (Vaccaro et al., 2025). The stronger coupling between  $\Psi_{stem}$  vs.  $\Psi_{trunk}$  in *D. lotus* ( $r^2 = 0.84$ ) compared to that observed in *D. virginiana* ( $r^2 = 0.64$ ) may partly reflect the wider range of water potential values reached by *D. lotus* during the water withholding period (Figs. 3 and 5).

Interestingly,  $\Psi_{trunk}$  showed the highest sensitivity in both rootstocks, followed by  $\Psi_{stem}$  and  $\Psi_{leaf}$  (Table 2). However, sensitivity values should be interpreted with caution, since the index S (SI/CV) integrates both treatment response and within-treatment variability. Therefore, high S values do not necessarily imply a stronger biological response, but may also reflect lower variability of the studied indicator. For this reason, the sensitivity ranking presented in Table 2 was interpreted together with the magnitude of the treatment response, the statistical significance of treatment effects, and the physiological consistency of each plant water status indicator. In this context, the high sensitivity of  $\Psi_{trunk}$ , together with its continuous and automated measurement, reinforces its usefulness as a practical indicator of persimmon water status under field conditions. Likewise, the relatively high sensitivity of  $\Psi_{stem}$  supports its reliability as a reference indicator of plant water status, whereas  $\Psi_{leaf}$  showed a more moderate responsiveness (Bellvert et al., 2016).

Sap flow (SF), measured using heat balance sensors installed on representative main branches, provided a functional indicator of transpiration dynamics under field conditions by quantifying heat dissipation associated with sap movement within the tree (Baker and Van Bavel, 1987; Steppe et al., 2015; Navarro et al., 2020). Our results showed that SF rates increased with evaporative demand (Fig. 2A) and decreased significantly under stress conditions (Figs. 4B–B'). Notably, SF was consistently lower in *D. lotus* than in *D. virginiana*, even under well irrigated conditions, while the relative reduction imposed in the  $T_{DI}$  treatment was greater in *D. virginiana*, consistent with its stronger stomatal regulation. Despite its physiological relevance, SF showed comparatively lower sensitivity (S) and higher variability (CV) than  $\Psi_{trunk}$ . Indeed, the weaker relationships between  $\Psi_{stem}$  vs. SF (Fig. 5B) and  $\Psi_{trunk}$  vs. SF (Fig. 6) reflect the strong influence of environmental drivers (i.e., VPD and solar radiation) as well as canopy size on plant transpiration (Wullschleger et al., 1998; Steppe et al., 2015, 2010), which may reduce the usefulness of SF as standalone indicator of drought stress under field conditions (Berdanier et al., 2016). Therefore, SF should be interpreted more as a functional indicator of plant water status rather than a direct proxy of persimmon water status.

Spectral indices showed limited responsiveness under the conditions of this study (Fig. 7). Although some differences between treatments were observed, their sensitivity (S) was generally low when field-variability was considered (Table 2). For *D. virginiana*, TCARI showed significant differences between  $T_{CTL}$  and  $T_{DI}$ , likely due to its sensitivity to leaf-level physiological adjustments (Haboudane et al., 2002). In *D. lotus*, CCCI was the most responsive UAV-derived index, which may reflect differences in chlorophyll status associated with rootstock vigour and canopy structure (Gitelson et al., 2003; Zarco-Tejada et al., 2013).

In contrast, canopy temperature ( $T_c$ ) was the UAV-derived indicator that most consistently reflected the water deficit imposed in this study. Its feasibility was supported not only by its relatively high S and low CV values, among the remote sensing indicators (Table 2) but also by the expected increase under water deficit conditions, consistent with reduced transpiration and evaporative cooling; its ability to discriminate irrigation treatments; and its coherence with the reductions observed in plant water status indicators such as  $\Psi_{stem}$  and  $\Psi_{trunk}$ . This response is physiological consistent, as  $T_c$  is directly linked to transpiration and  $g_s$

through evaporative cooling (Jones, 2004; González-Dugo et al., 2006; Conesa et al., 2019), allowing it to capture short-term physiological responses to water deficit more effectively than spectral indices in both rootstocks (Fig. 7 and Table 2).

The limited performance of spectral indices likely reflects the dominant influence of canopy architecture, leaf area distribution and biochemical traits on reflectance sensing signals, which can mask short-term stress responses to water (Berni et al., 2009; Zarco-Tejada et al., 2013). This effect was particularly evident in *D. lotus*, where higher sensitivity of ground-based indicators suggests stronger physiological responses that were not equally captured by multispectral data. Similar limitations have been reported in orchards with partial canopy cover and heterogeneous backgrounds (Xue and Su, 2017; Conesa et al., 2019), which highlights the constraints of instantaneous remote sensing for detecting moderated water deficits as reported by Conesa et al., 2019, who also indicated that more severe or longer water stress conditions may be required to enhance the sensitivity of spectral indices.

Finally, our results showed that UAV-based and ground-based measurements provide complementary information on plant water status. Whilst  $T_c$  can capture short-term stress signals, spectral indices can be better suited for monitoring structural or nutritional status, especially in *D. lotus*.  $\Psi_{\text{stem}}$  and  $\Psi_{\text{leaf}}$  also proved to be reliable reference plant water status indicators. However, due to the potential for automation, the combination of  $\Psi_{\text{trunk}}$  validation with SF measurements proved to be a promising alternative for accurately monitoring the water status of persimmons, regardless of rootstock, under semi-arid Mediterranean conditions.

## 5. Conclusions

Overall, the results of this study show contrasting drought response strategies between the studied rootstocks. *D. lotus* showed physiological responses consistent with a more anisohydric-like behaviour, maintaining relatively open stomata and stable leaf gas exchange despite the observed significant decline in  $\Psi_{\text{stem}}$ ,  $\Psi_{\text{leaf}}$  and  $\Psi_{\text{trunk}}$ . In contrast, *D. virginiana* showed a more isohydric-like physiological response, with earlier stomatal closure and a more conservative hydraulic strategy that limited the decrease in plant water potentials under water deficit conditions. These findings highlight that rootstock selection is a crucial factor determining drought resilience in persimmon trees. Under the conditions of this study, *D. virginiana* exhibited a more effective adaptive response to water deficits and could therefore be considered a more suitable rootstock for semi-arid conditions, even if further agronomic studies are required.

Among the evaluated indicators, continuous  $\Psi_{\text{trunk}}$  measurements provide the most reliable information on plant water status, whereas canopy reflectance indices are less sensitive to short-term stress changes. In this regard, the use of MTs, particularly in combination with SF measurements, proved to be a robust, non-destructive, and automated approach for precise irrigation management in persimmon orchards.

The integration of continuous soil- and plant-based monitoring with UAV-derived canopy information demonstrated the potential multi-scale approaches for improving water status assessment under precise irrigation conditions. However, the UAVs assessment performed in this study should be interpreted as a complementary snapshot evaluation under peak summer stress conditions rather than as a broad temporal validation of remote sensing indicators. Although, UAVs provide immediate spatial information and capture relevant physiological responses to water stress, the discrete nature of these measurements limits their use for accurate monitoring of persimmon water status, particularly in the case of *D. lotus*. Therefore, their interpretation requires a solid understanding of plant physiological responses, and it should be integrated with continuous soil-plant-based sensing approaches.

## CRedit authorship contribution statement

**María R. Conesa:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Writing – original draft, Writing – review & editing. **Wenceslao Conejero:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – review & editing. **Margarita Parra:** Investigation, Resources, Writing – review & editing. **Alejandra Navarro:** Investigation, Methodology, Validation, Writing – review & editing. **Diego S. Intrigliolo:** Validation, Writing – review & editing. **M. Carmen Ruiz-Sánchez:** Conceptualization, Funding acquisition, Investigation, Project administration, Supervision, Writing – review & editing.

## 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.

## Acknowledgments

This research was part of the projects: (i) SP-IRRICROP (PID2023-147690OB-I00) funded by Spanish State Research Agency MCIU/AEI/10.13039/501100011033/FEDER-UE, (ii) BRILLASENS FSRM/10.13039/100007801(22605/PI/24) and (iii) (23029/GERM/25), funded by Seneca Foundation- Region of Murcia. The authors are very grateful to Juan Vera (CEBAS-CSIC) and Cristina Castillo (CTCON) for their support in sensor data acquisition and remote sensing imagery analysis, respectively.

## Data availability

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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