Agricultural Water Management 316 (2025) 109607

Contents lists available at ScienceDirect

Agricultural Water Management

journal homepage: www.elsevier.com/locate/agwat

Combining plant-based sensing and mechanistic modelling to quantify hydraulic resistance and capacitance for real-time irrigation in Mediterranean yellow-fleshed kiwifruit orchards

Maria Calabritto [a], Alba N. Mininni [a,*], Dirk J.W. De Pauw [c], Steve Green [d], Bartolomeo Dichio [a], Kathy Steppe [b,*]

[a] Department of Agricultural, Forest, Food, and Environmental Sciences, University of Basilicata, Potenza, Italy
[b] Laboratory of Plant Ecology, Department of Plants and Crops, Faculty of Bioscience Engineering, Ghent University, Coupure links 653, Ghent B-9000, Belgium
[c] Plant AnalytiX, Beekstraat 23B, Mariakerke, B-9000, Belgium
[d] New Zealand Institute for Plant and Food Research Limited, Palmerston North, New Zealand

ARTICLE INFO

Handling Editor: Dr. Brent Clothier

Keywords:
Sap flow
Plant sensors
Water flow model
Drought stress
Embolism formation
Irrigation decision
Kiwifruit

ABSTRACT

Climate change and increasing water scarcity, especially in the Mediterranean region, are major challenges for modern agriculture, requiring the implementation of real-time irrigation management methods to improve whole-plant water use efficiency. In the present study, two plant-based measurements (trunk sap flow and trunk water potential, ψ_{trunk}) were used in combination with a dynamic water flow model to estimate hydraulic capacitance (C) and hydraulic resistance (R) along the water transport pathway in yellow-fleshed kiwifruit vines grown in a Mediterranean environment under both well-watered and drought conditions. A sensitivity analysis of the model was performed to select a subset of identifiable parameters, accounting for most of the variability in model predictions of ψ_{trunk}. Based on the identifiable parameters, two model calibrations were performed: (1) model calibration of C and R; (2) model calibration of C, R and the initial amount of water stored in the stem compartment. These parameters were recalibrated daily based on a 1-day moving window. The best model performance under soil water limiting conditions was achieved when all three parameters were used for calibration. C and R parameters strongly correlated with ψ_{trunk}, revealing the hydraulic behavior and drought response of kiwifruit vines. In particular, C was found to decrease with more negative ψ_{trunk} values, whereas R showed an increase. In addition, C and R varied within a narrow range of ψ_{trunk} fluctuations, as occurred in well-watered vines. While the proposed modelling approach requires investments in sensor technologies and a data management and modelling platform, it offers the potential to quantify and visualize daily dynamics in plant hydraulic parameters and provide farmers with valuable tools to improve real-time management of irrigation in the era of precision agriculture.

1. Introduction

In the current climate change scenario, the Mediterranean region is recognized as one of the world's water crisis hot spots due to significant increases in temperatures and decreases in rainfall (with fewer events but of greater intensity), threatening water availability throughout the region (Milano et al., 2013; Lionello and Scarascia, 2018; Prada et al., 2024). Climate change affects crop phenological stages and irrigation water requirement, and increases the frequency of extreme weather events, such as droughts and heat waves (Soares et al., 2022). In this specific climatic context, kiwifruit needs to face high temperatures, irradiance and leaf-to-air vapor pressure deficit during summers (Montanaro et al., 2009). In particular, the kiwifruit species belongs to the lianas and has developed peculiar morpho-anatomical traits and hydraulic system features adapted to its native habitats, which are characterized by moderate light intensity and abundant rainfall (1200–1800 mm year^{-1}) (Ferguson, 1984), ensuring non-limiting water conditions. Sparse and large xylem vessels (200–350 μm in diameter) contribute to low xylem hydraulic resistance to vertical water flow and allow large amounts of water to be transported upwards, with very high

* Corresponding authors.
E-mail addresses: alba.mininni@unibas.it (A.N. Mininni), kathy.steppe@UGent.be (K. Steppe).

https://doi.org/10.1016/j.agwat.2025.109607
Received 12 April 2025; Received in revised form 10 June 2025; Accepted 10 June 2025
Available online 13 June 2025

stem hydraulic conductivity (Dichio et al., 2013). Large leaves, which provide a wide transpiring surface, contribute to high daily transpiration rates, reaching approximately 40–60 L day^{-1} in a Mediterranean kiwifruit orchard (Dichio et al., 2013; Green et al., 2022; Xiloyannis et al., 2023). The vascular tissue is composed of semi-ring porous wood, which contributes to low axial xylem resistance (Condon, 1992). The high leaf-specific whole-plant conductance (i.e., whole-plant conductance normalized by leaf area, Dichio et al., 2013) of kiwifruit vines compared to olive plants, which is attributable to the larger conducting vessels, could contribute to the high susceptibility of this species to embolism formation under drought conditions (Dichio et al., 2013), generally exacerbated by high temperatures and high evaporative demand. Clearwater and Clark (2003) reported that embolism formation occurs more frequently when xylem tensions are high, and less frequently when drought stress is relieved. They also found that embolism formation occurs more frequently and at lower xylem tensions in *Actinidia* vines than in *Ripogonium*. In-depth studies of water flow dynamics, plant water status and drought susceptibility have become urgent challenges that need to be addressed in the current climate change scenario, as more extreme drought events are expected to occur in the coming years (Da Sois et al., 2024) and irrigation water supply cannot be guaranteed at all times. As soil water content decreases, hydraulic resistance to water transport through the soil increases and soil matric potential decreases, creating adjusted water potential gradients within the plant that drive water flow (Scharwies and Dinneny, 2019). As plants respond differently to water deficit (Scharwies and Dinneny, 2019), information on the plant hydraulic resistance encountered in the soil-plant continuum and its changes due to drought stress conditions is important as it strongly influences plant water status and helps to understand important plant processes occurring under these conditions (Baert et al., 2015).

The high water requirements of kiwifruit (Chartzoulakis et al., 1993; Holzapfel et al., 2000; Calderón-Orellana et al., 2021) and its susceptibility to water deficits (Judd et al., 1989; Montanaro et al., 2007; Mills et al., 2009; Calderón-Orellana et al., 2021) highlight the importance of effectively and properly quantifying irrigation requirements and identifying water stress indicators and thresholds. Proper irrigation management helps to mitigate the adverse effects of environmental stressors caused by climate change (Rajan et al., 2024). It limits midday depression in physiological parameters, such as photosynthetic rate, and sunburn of fruits and leaves, which are exacerbated by increasing temperatures and radiation during the hottest hours of the day (Gucci et al., 1996; Montanaro et al., 2009; Wu et al., 2023) and pose a threat to kiwifruit production in Mediterranean environments. The implementation of innovative plant-based irrigation management methods can be of great importance to kiwifruit contributing to a more precise irrigation for this crop. Precision irrigation, driven by data on soil water status, plant responses and weather variables, delivers water at the right time and in the right amount, contributing to water saving, improvement of whole-plant water use efficiency and timely fulfilment of crop water needs (Bwambale et al., 2022). Furthermore, delivering the right amount of irrigation water to meet the crop's needs at different times, also limits the onset of transient drought stress (Brahmanand and Singh, 2022), which can easily occur throughout the day especially in arid and semi-arid environments. Several soil and plant sensors have been suggested as effective irrigation tools, and trunk diameter variations, sap flow and plant water potential are the most commonly used plant sensors in scientific studies (Moriana et al., 2012). Plant water status monitoring, integrated with soil and environmental information, can support precision irrigation and inform irrigation scheduling (McCutchan and Shackel, 1992; Goldhamer et al., 1999; Intrigliolo and Castel, 2004; Ortuño et al., 2010; Shackel, 2011). Plant physiological and drought stress indicators are therefore increasingly accepted and used by farmers as useful diagnostic tools (Fereres and Evans, 2006; Noun et al., 2022).

Despite significant advancements in soil- and plant-based sensors, which enable continuous monitoring and provide real-time feedback on soil and plant water status, enhancing our understanding of plant responses to different soil and environmental conditions and enabling more accurate irrigation management, the widespread adoption of effective real-time decision support methods for irrigation is still lacking. A significant gap between current irrigation practices and what is considered best practice in most cases is observed and remains a major concern (Fereres and Evans, 2006).

This gap can be filled by integrating plant measurements and mechanistic modelling to develop novel plant-based irrigation scheduling methods (Steppe et al., 2008; Steppe, 2013). Although such models are already available in the scientific literature and thoroughly validated (Steppe et al., 2006, 2008; De Pauw et al., 2008a), their practical application in irrigation scheduling has not yet been fully exploited. Moreover, modelling plant water transport dynamics during drought stress can deepen our understanding of the underlying processes and mechanisms plants use under such conditions (Steppe et al., 2008; Baert et al., 2015; De Swaef et al., 2022). This knowledge is particularly important in the climatically challenging Mediterranean region, where it can help assess the impacts of climate change on crop performance.

The present study integrates continuous plant measurements from sensors, such as trunk sap flow and trunk microtensiometers, with a mechanistic water flow model to achieve the following objectives: (i) simulate trunk water potential dynamics (ψ_{trunk}) to predict changes in hydraulic capacitance (C) and resistance (R) of yellow-fleshed kiwifruit vines under well-watered and drought conditions in a Mediterranean climate; (ii) provide practical insights into model calibration for more accurate estimation of key hydraulic parameters, especially under drought conditions; and (iii) illustrate the potential of the mechanistic model as an effective tool for plant-based, real-time irrigation scheduling in fruit crops.

2. Materials and methods

2.1. Plant material and experimental site

The experiment was carried out during the 2023 growing season in a commercial and mature kiwifruit orchard (*Actinidia chinensis* var. *chinensis*, cv. Zesy002) planted in 2014 in Metaponto (South Italy, 40°24'N 16°46'E) over a 4-week period from August 2 till 15 September (from Day-of-the Year (DOY) 214 until DOY 258). The yellow-fleshed kiwifruit cultivar was grafted onto D1 rootstock (*A. chinensis* var. *deliciosa*), cultivated at 5 m x 2 m spacing and trained as a pergola system. The soil profile consisted of a uniform sandy clay loam texture (58 % sand, 14 % silt and 28 % clay). The experimental plot consisted of two irrigation blocks equipped with independent valves and analogue flow meters. A manual flow meter (TEV58R GU-SD, Greiner S.p.A., Italy) was used to record the irrigation volumes distributed and an automatic irrigation controller ("Irrifarm" system, Pan. Agri S.r.l., Italy) was used to remotely control the water supply. Irrigation was provided by micro-sprinklers with a 5 m x 1 m spacing in the vine row, using a single auto-pressure compensating emitter per vine at a flow rate of 40 L h^{-1} and a wetted radius of 0.9 m.

2.2. Irrigation scheduling and treatments

All vines were grown under optimal soil water availability conditions throughout the season until the beginning of the experiment. Daily vine water requirements (crop evapotranspiration, ET_c) were estimated using reference evapotranspiration (ET_0) and crop coefficient (K_c) (Allen et al., 1998), with K_c ranging from 0.5 to 1.1 along the season (Steduto et al., 2012). The irrigation requirement was calculated using the following equation:

$$IR = (ET_c - ER)/ime \quad (1)$$

where IR is the irrigation requirement (mm), ET_c is the crop evapotranspiration (mm), ER is the effective rainfall [calculated by considering daily rainfall < 5 mm as ineffective (Dastane, 1974)], and ime is the irrigation method efficiency (0.95). The soil volume wetted by irrigation was calculated considering the sprinkler wetting radius, the depth of the wetting pattern (0.6 m) and the number of emitters per hectare. The irrigation requirement was adjusted weekly based on continuous monitoring of the water content by soil moisture probes. Real applied irrigation volumes were derived from increases or decreases in irrigation requirement in order to maintain the soil moisture level of the soil volume wetted by irrigation within field capacity (FC) and readily available water (RAW) (Mininni et al., 2022; Calabritto et al., 2024). Two irrigation treatments were applied: a well-watered irrigation treatment, in which irrigation returned 100 % of irrigation volume defined according to the vines' water need and soil moisture monitoring, and a drought irrigation treatment, in which irrigation was reduced to develop progressive levels of drought stress. In particular, the well-watered irrigation treatment received daily irrigation volumes of 45 m^3ha^{-1} (DOY 214–216; DOY 222–229; DOY 241–253) and 60 m^3ha^{-1} (DOY 217–221; DOY 230–240; DOY 254–258) throughout the experimental period. Daily irrigation volumes were split into three/four irrigation events throughout the experiment, except for the period from DOY 220 to DOY 237, where irrigation volumes were split into only one or maximum two events per day (early in the morning and late in the afternoon). In contrast, in the drought treatment, irrigation was first ceased (DOY 220–226) and then reduced (DOY 227–236, 15 m^3ha^{-1}) with full re-watering on DOY 237, and then ceased again (DOY 244–255) with full re-watering on DOY 256. In the drought irrigation treatment, daily irrigation volumes were distributed in a single intervention from DOY 227 to DOY 237.

2.3. Environmental and soil measurements

Environmental variables, such as daily ET_0, minimum, maximum and mean air temperature, relative humidity and net solar radiation were recorded by a regional meteorological station located about 1 km from the experimental field. Hourly air vapor pressure deficit (VPD) was calculated using hourly values of air temperature and relative humidity (Goudriaan and van Laar, 1994). ET_0 was calculated using the Penman-Monteith equation (Allen et al., 1998).

Frequency domain reflectometry (FDR) 90 cm multi-profile soil moisture probes (Drill & Drop, Sentek Sensor Technologies, Stepney, Australia) were used to continuously monitor the volumetric soil water content (θ, cm^3 cm^{-3}) in 10 cm increments throughout the soil vertical profile, allowing the remote detection of instantaneous oscillations in each soil layer. A soil layer of 0–60 cm was monitored in the present study, as this depth has been previously reported to be useful for irrigation purposes in kiwifruit based on soil type and root development and uptake activity (Xiloyannis et al., 2023; Calabritto et al., 2024). The probes were installed in the row at a distance of 0.5 m from the vine trunk and approximately in the center of the wet soil volume.

The relation between θ and the matric potential (h) was investigated through the water retention curve obtained with the Richards' pressure plates apparatus (Richards, 1948) in the 0–60 cm soil profile. Hydraulic characterization of the soil was conducted by fitting measurement data to the van Genuchten equation (1980) (Fig. 1).

Based on estimated parameter values (Table 1), the matric potential of the soil (ψ_{soil}, MPa) can be calculated using the equation of van Genuchten (1980):

$$\Psi_{soil} = \frac{1}{\alpha}\left[\left(\frac{\theta-\theta_r}{\theta_s-\theta_r}\right)^{\left(-\frac{1}{m}\right)} - 1\right]^{\frac{1}{n}}$$

where θ_r and θ_s are the residual and saturated volumetric water content (cm^3 cm^{-3}), respectively, α (cm^{-1}), n (dimensionless) and m = 1–1/n

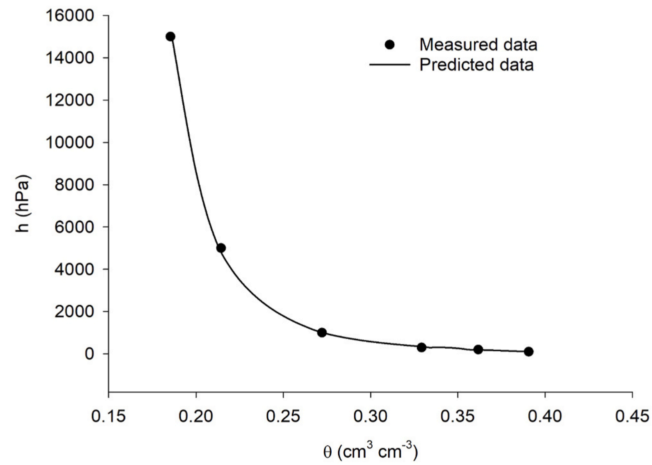

Fig. 1. Water retention curve of the sandy clay loam soil profile (0–60 cm). The van Genuchten function was fitted to the water retention data.

Table 1
Estimated parameters of the van genuchten (1980) equation for the studied kiwi orchard.

Parameter	Estimation
θ_s (cm^3 cm^{-3})	0.3974
θ_r (cm^3 cm^{-3})	0.1891
α (cm^{-1})	0.0115
n (-)	1.3086
m (-)	0.2358

(Mualem, 1976) the form parameters.

2.4. Plant sensor measurements

Trunk water potential (ψ_{trunk}, MPa) of kiwifruit vines was continuously monitored by microtensiometers (FloraPulse, Davis, CA, USA) embedded directly in the trunk. The sensors were installed at pre-dawn and reached equilibrium with the vine xylem within a few days after installation (Pagay, 2022). Data of ψ_{trunk} were collected at 20 min intervals, stored in a memory card inserted into the solar powered wireless data logger and uploaded to a cloud repository. Trunk microtensiometers were installed in the field on two vines for each irrigation treatment (well-watered and drought).

Trunk sap flow (SF, kg h^{-1}) was measured in four vines for each irrigation treatment. The selected vines had straight trunk sections and showed uniform canopy dimensions. Each vine was instrumented with a single set of three-channel sensors (model HP3TC, Tranzflo NZ Ltd, Palmerston North, New Zealand). The probes were installed in each trunk at a height of approximately 0.75 m above the ground. One temperature probe (the main sensor) and a second probe (the reference sensor) were positioned 15 mm and 40 mm, respectively, downstream of the heater probe. The vine trunk close to the sensors was wrapped in aluminum foil for thermal and light insulation. Sap flux density was measured using the T-max heat-pulse method (Cohen et al., 1981; Green et al., 1989, 2003) with a slight change in sensor spacing (5 mm larger distance between the heater and the sensor) to cope with the very high sap flux densities (J_S < 200 cm h^{-1}) expected in kiwifruit vines during the middle of the day. The wider sensor spacing also improves the resolution of low flow rates down to about 1 cm h^{-1} (Green et al., 2003). A data logger (model CR1000, Campbell Scientific, Logan, USA) was used to check the heater output and to measure the time of maximum temperature rise after the application of a short (4 s) heat pulse. Sap flux densities were calculated from the time values of maximum temperature rise, including a wound correction factor to account for the effect of wounding caused by the probes (a wound diameter of 2.8 mm was assumed for the 2.0 mm diameter drill holes; Green et al. 2022). Data of SF were collected at 30 min intervals.

2.5. Model description

An existing mechanistic water flow and storage model (Steppe et al., 2006, 2008), which describes water transport dynamics in individual plants, was adapted in the present study (Fig. 2).

The basic principles of the original water flow and storage model have been maintained to simulate changes in the ψ_{trunk} of a group of kiwifruit vines for each irrigation treatment. Continuously measured sap flow in the trunk (SF) and soil matric potential (ψ_{soil}), which is considered as a limiting external water storage pool, were used as inputs to the model. The model, which was simplified to describe the processes occurring in the stem compartment, consisted of a stem storage compartment (i.e., a stem storage pool including the living cells of the stem bark) and a vertical xylem flow path (i.e., F_{trunk}). The stem storage compartment was characterized by its hydraulic capacitance (C), which is defined as the ratio of the change in the amount of water present in the stem storage tissue (W) to the change in water potential of the tissue (Steppe et al., 2006). As transpiration starts in the morning ψ_{trunk} decreases, establishing a water potential gradient between stem and soil which induces water uptake from the soil. The developed water potential difference along the non-living xylem vessels forces water to move upwards, inducing a vertical water transport (Steppe et al., 2006; De Pauw et al., 2008a). Since the living tissues of the stem storage pool and the xylem are hydraulically connected, the water potential difference between the xylem and the bark induces a radial water flow allowing internally stored water to contribute to the transpiration stream (Genard et al., 2001; Steppe et al., 2006, 2015a). As a result of the radial water flow, W varies. Furthermore, as water ascends, it encounters resistance in the form of hydraulic flow resistance within the xylem. The model developed by Baert et al. (2015) incorporates a variable integrated hydraulic resistance that captures the entire water transport pathway from soil to stem, which accounts for changes in overall hydraulic resistance in the soil-to-stem segment and is related to ψ_{soil}. In our study, the adapted model integrates the resistances of the soil, roots and trunk into a single parameter, R.

2.6. Model calibration and simulation

Model simulation, calibration and identifiability analysis were performed using the plant modelling software PhytoSim (Plant AnalytiX, Mariakerke, Belgium) for each irrigation treatment. All model equations were solved using a fourth order Runge Kutta fixed step size integrator (fixed step size= 0.1 h). Model calibration was based on the Shuffled Complex Evolution (global search method) and used to minimize the weighted sum of squared errors between the model output and the measured data for ψ_{trunk}. Continuous measurements of ψ_{trunk} were used as calibration variable. An identifiability analysis of the model was performed to select a subset of identifiable parameters (De Pauw et al., 2008a). A model parameter subset is considered identifiable when the collinearity index remains below 15, indicating limited linear dependency among the parameters, and the parameters demonstrate high influence on the model output. While model output sensitivity lacks a definitive threshold, it serves as a useful ranking criterion for comparing potentially identifiable parameter subsets, and can help selecting the most appropriate subset (De Pauw et al., 2008a). Three identifiable key model parameters (i.e., calibration parameters) were found to influence ψ_{trunk}: the capacitance of the water storage tissue in the stem compartment (C), the hydraulic xylem resistance (R) and the initial value of the water content in the stem storage tissue (W). The remaining non-identifiable model parameters were set at a fixed value taken from the literature or directly calculated. Two types of model calibration were performed using the two distinct datasets, representing the well-watered and the drought irrigation treatments. Simulations of ψ_{trunk} were performed with only two calibration parameters (C and R) and with all three calibration parameters (C, R and initial W) for both irrigation treatments to compare the simulated pattern of ψ_{trunk} and analyze differences in the calibrated parameters. First model calibration was performed on DOY 214. The identifiable parameters were recalibrated daily based on a 1-day moving window (Steppe et al., 2008), which shifts daily using both initial conditions and parameters from the previous calibration for subsequent model simulations. This ensured a good model fit at all times, allowing investigation of the daily variability of the calibrated parameters in response to changes in ψ_{trunk}.

3. Results

3.1. ψ_{trunk} simulated with fixed or calibrated initial W

The experimental days were characterized by generally sunny and dry weather with high evaporative demand. VPD was quite variable throughout the experimental days, reaching maximum hourly values ranging from 1.85 kPa to 5 kPa observed on DOY 216 and 236,

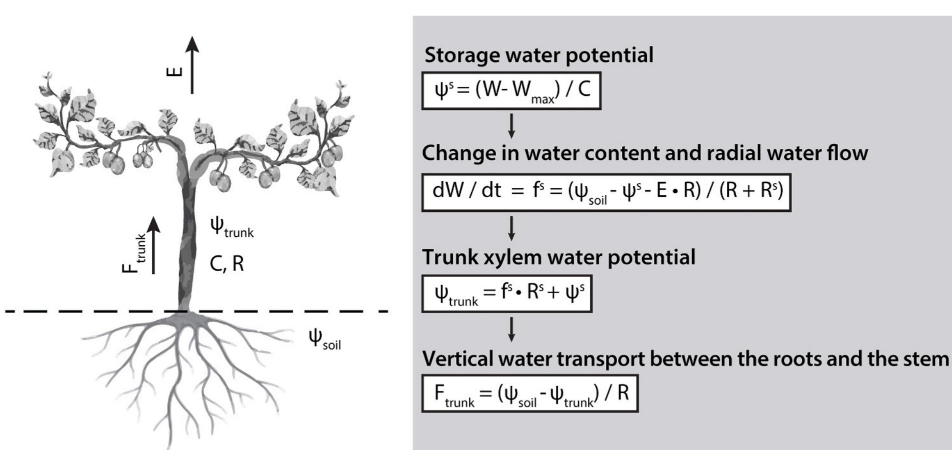

Fig. 2. Schematic representation and mathematical equations of the dynamic water flow and storage model from Steppe et al., 2008. The model consists of an internal water storage compartment (stem) and external water source (soil) and a flow path (F_{trunk}). The model is driven by transpiration (E) and soil water potential (ψ_{soil}) to determine the hydraulic capacitance of the stem storage compartment (C) and xylem hydraulic resistance (R). Abbreviations in the scheme: W = water content in the storage compartment; W_{max} = maximum water content in the storage compartment (38 kg); R^s = hydraulic resistance of the storage compartment (0.01 MPa h kg^{-1}); ψ_{trunk} = trunk water potential; ψ^s = stem storage water potential; f^s = radial water flow.

respectively. Daily ET_0 values ranged between 3.6 mm and 7.8 mm (Fig. 3a). Maximum air temperatures exceeded 32 °C on 27 of the 45 days, while minimum air temperatures varied between 14 °C and 26 °C (Fig. 3b). Daily net solar radiation values ranged between 2.4 MJ m^{-2} and 12.1 MJ m^{-2} during the experimental days and reached a maximum value of 12.1 MJ m^{-2} on DOY 216 (Fig. 3c). Irradiance, air temperature, vapor pressure deficit and environmental demand were typical of Mediterranean climates (Seager et al., 2019).

Calculated and continuously measured soil water potential (ψ_{soil}) and sap flow (SF) from the well-watered (Fig. 4a) and drought (Fig. 4b) irrigation treatments were used as inputs to the model. Sap flow reflected environmental and soil water content changes during the days of the experiment. Transpiration during the night hours occurred in both irrigation treatments on days when higher VPD values were observed during the night (Fig. 3a). In the drought-stressed kiwifruit vines, the measured sap flow decreased with declining soil water availability, as indicated by the decrease in soil water potential, which was less pronounced in the first drought phase (from DOY 220 to DOY 226) and more pronounced in the subsequent drought phase (from DOY 244 to DOY 255). Upon full re-watering (from DOY 237 to DOY 243), sap flow of drought-stressed kiwifruit vines showed a slight increase again (Fig. 4b).

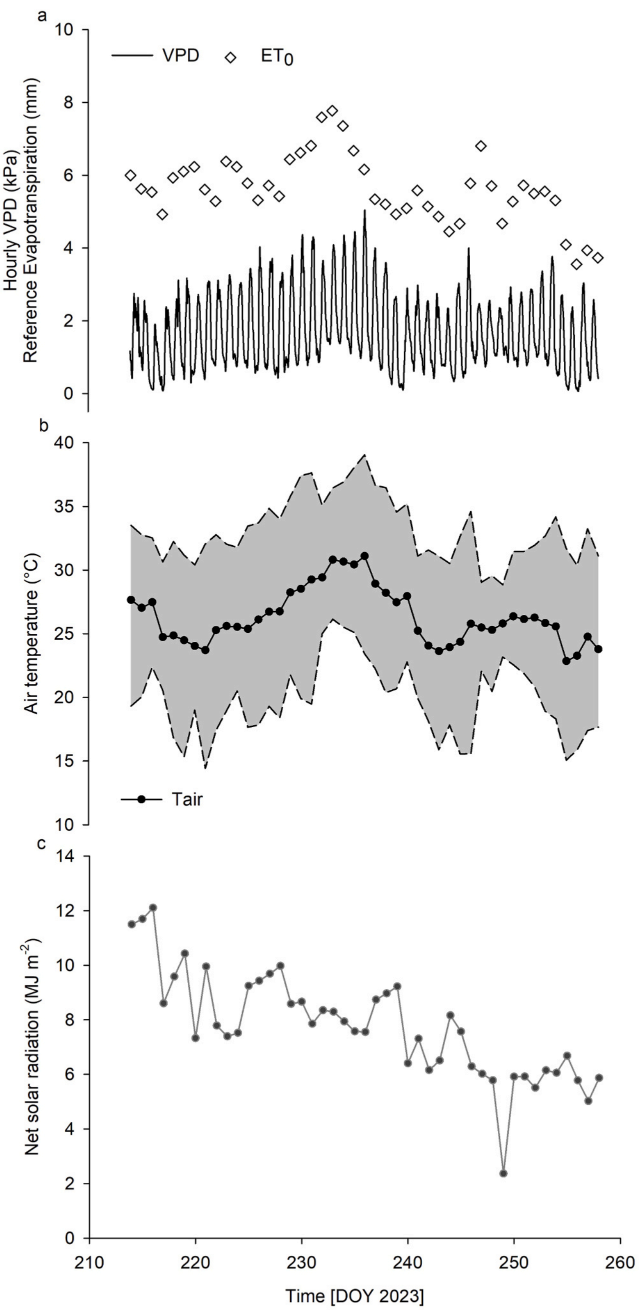

Fig. 3. (a) Hourly vapor pressure deficit (VPD) and daily reference evapotranspiration (ET_0), (b) daily air temperature (maximum, minimum and mean), (c) average daily net solar radiation during the irrigation experiment in a Mediterranean kiwifruit orchard. Time is expressed in day of the year [DOY].

The measured trunk water potential (ψ_{trunk}) of the well-watered vines showed values ranging from −0.02 MPa to −0.54 MPa, with daily oscillations and changes in the pre-dawn values, which can be partly attributed to the irrigation scheduling, in particular to changes in the irrigation volume and the splitting of the daily irrigation volume. The progressive drought stress developed in the drought irrigation treatment led to a decrease in ψ_{trunk}, reaching minimum values around −1.1 MPa in both drought phases, but with a different evolution of the stress within the plant, as shown by the differential response of ψ_{trunk}. Mechanistic modelling, which simulated stem hydraulics, provided ψ_{trunk} variations that matched closely with those measured in both well-watered and drought irrigation treatments (Fig. 5). The kiwifruit ψ_{trunk} model was calibrated using ψ_{soil} and SF as input variables and hydraulic capacitance (C) and resistance (R) as the calibrated parameters (Fig. 5a, b), or with C, R and the initial amount of water stored in the stem compartment (W) as calibrated parameters (Fig. 5c, d). The simulated ψ_{trunk} varied according to the different types of calibration in both irrigation treatments. In the case of the well-watered treatment, a good fit between the simulated and measured ψ_{trunk} was observed in both calibrations based on only two (C and R) (Fig. 5a) or all three parameters (C, R and initial W) (Fig. 5c). When the initial value of W was included as a calibration variable, the simulations compared with the measured data showed that ψ_{trunk} became more responsive, with peaks associated with the daily recalibration of the amount of water present in the stem storage tissue, as illustrated in the detailed panels of Fig. 5 (I-II). While the simulation results of the two types of model calibration were both good for the well-watered treatment, more pronounced differences between the simulation results were observed for the drought treatment. In particular, the model calibration performed with only two parameters (C and R) was not sufficient to achieve a good comparison between the simulated and measured ψ_{trunk} during the second, more severe drought phase (from DOY 244 to DOY 255) (Fig. 5b). A distinct improvement in simulating the decreasing trend in ψ_{trunk} of the drought-stressed kiwifruit vines was achieved by including the initial value of W as a parameter in the calibration process. This resulted in a better fit between the simulated and measured ψ_{trunk} also during the second drought phase (Fig. 5d), compared to the model calibration with only C and R, which failed to describe the vine responses to severe drought, as detailed in the panel of Fig. 5 (III).

3.2. *Variability of C and R in response to ψ_{trunk}*

Clear linear relationships were found between the measured daily average ψ_{trunk} and the C and R values obtained from the model calibration performed with all three parameters (C, R and initial W), which were recalibrated daily based on a 1-day moving window (Fig. 6). In particular, C and ψ_{trunk} were linearly positively correlated, suggesting that improved plant water status is associated with an increase in stem storage tissue capacitance, whereas R and ψ_{trunk} were linearly negatively correlated, suggesting that reduced plant water potential implies an increase in the hydraulic resistance. A weaker relationship was found for C by combining data from both the drought and well-watered irrigation treatments. Grey data points above the linear regression indicate a greater increase in the hydraulic capacitance of the stem water storage tissue due to re-watering of the drought stress treatment, which was carried out between DOY 237 and DOY 243. For C, these data points were excluded from regression calculation due to a different underlying

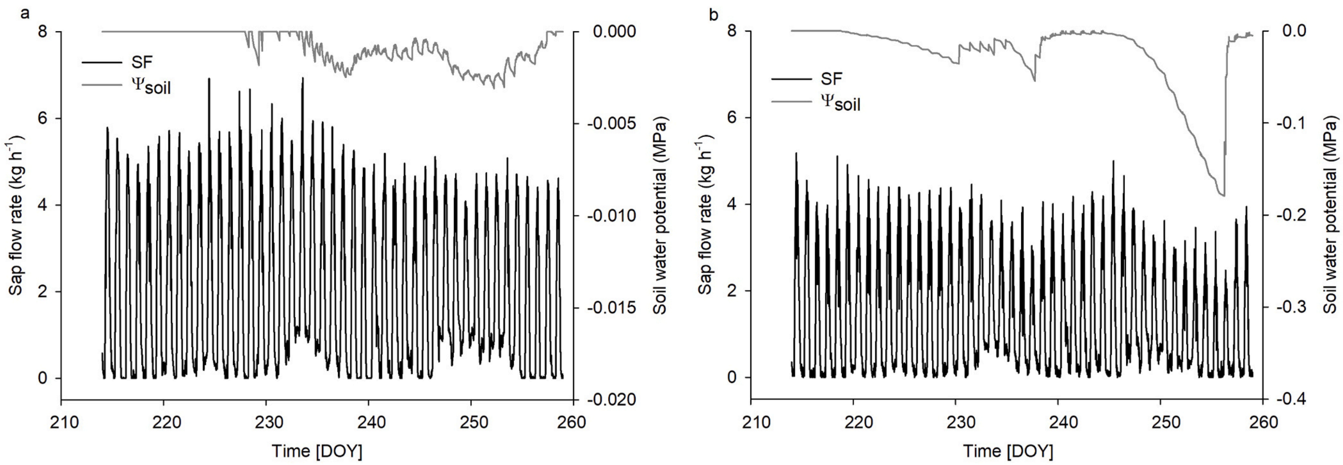

Fig. 4. Inputs used in the trunk water potential modelling process: sap flow rate (SF, black line) and soil water potential (ψ_{soil}, grey line) in the (a) well-watered and the (b) drought irrigation treatment. Time is expressed in day of the year [DOY].

process. The re-watering phase in the drought treatment allowed the vines to recover their ψ_{trunk}, which returned to the range of control values, and to increase their capacitance (Fig. 6a). Instead, a stronger relationship was found for R, combining data from both the drought and well-watered irrigation treatments (Fig. 6b). However, clear relationships were also maintained in the well-watered treatment for both C and R parameters, as shown in the detailed panels of Fig. 6 (I-II), indicating that changes in hydraulic capacitance and resistance also occurred within a narrow range of changes in ψ_{trunk}.

Daily model calibration, which was performed using ψ_{trunk} measurements and a 1-day moving window, showed variation in both the hydraulic capacitance and resistance values (Fig. 7a, b). This adjustment of the parameter values was necessary to ensure a good model fit on all days (Fig. 5). The lowering of ψ_{trunk} in the drought-stressed vines during the drought periods resulted in lower C (Fig. 7a) and higher R values (Fig. 7b) compared to the well-watered vines. The hydraulic capacitance of drought-stressed vines showed lower values during the first drought period, a steeper increase in values due to full re-watering (i.e., from DOY 237 to DOY 243), before decreasing again, but to values that remained in the range of those of well-watered vines (Fig. 7a). On the other hand, the hydraulic resistance increased progressively during the first drought period, suggesting a progressive development of drought stress within the plant, and showed a steeper increase during the second drought period, peaking at values of 0.87 MPa h kg^{-1}, suggesting a more rapid and severe establishment of stress (Fig. 7b). Although the daily R values remained in a small range from 0.06 to 0.12 MPa h kg^{-1} under adequate soil water availability, a daily variability in hydraulic resistance was observed (Fig. 7b), highlighting the responsiveness of the parameter, which can contribute to the understanding of plant behavior, according to the relationship found with ψ_{trunk} in the well-watered treatment (Fig. 6, panel II).

3.3. *Comparison of calibrated model parameters*

The calibrated model parameters (C and R) did not vary between the two types of model calibration (i.e. based on only two or three parameters by including the initial value of W in the calibration process) in the well-watered dataset (Fig. 8a, b). On the other hand, a different dynamic of C and R parameters was observed when comparing model calibrations under more severe drought conditions. In this case, the model calibration performed with only two parameters was not able to provide reliable calibrated values of C and R (see peaks, Fig. 8c, d). Differences in the calibrated model parameters between the two types of model calibration explained the failure of the two-parameter based model calibration to simulate ψ_{trunk} when severe drought occurred, and supported the improvement in the calibrated values (C and R) when the initial value of W was included in the calibration process, which also allowed a better simulation of ψ_{trunk} (Fig. 5b, d).

The two model calibration approaches differed in that one kept the initial value of W fixed at the value obtained from the end of the previous 1-day moving window, while the other included the initial value of W as a calibration parameter that was recalibrated daily together with C and R. Again, the comparison of the initial W values between these model calibration approaches showed no relevant differences for the well-watered dataset (Fig. 9a). However, during severe drought, the two-parameter model calibration with a fixed initial W value failed, as shown by negative initial W values (Fig. 9b).

4. Discussion

4.1. *Practical insights into model calibration*

An existing water flow and storage model (Steppe et al., 2006; 2008), originally designed to simulate stem water potential among other variables, was adapted for use in this study to simulate trunk water potential and estimate hydraulic parameters associated with water flow in kiwifruit under drought stress. The model uses continuously measured sap flow and soil water potential data as inputs, while trunk water potential measurements are used for calibration. As the trunk water potential was measured continuously, it was possible to derive the hydraulic capacitance and resistance of kiwifruit vines on a daily basis under well-watered and progressive drought conditions, which helps to understand the physiology of kiwifruit vines and to determine the trends and order of magnitude of key plant hydraulic parameters. The adapted model was able to simulate the measured data (Fig. 5). Distinct improvements in the simulation of trunk water potential changes under drought stress were obtained by accurately choosing the size of the moving window, which is an important issue to consider when performing model calibration (Steppe et al., 2008), and the parameters to be considered for calibration purposes. In particular, for a successful application of the mechanistic model in the present study, a moving window of small size (i.e., 1 day) was chosen. This window size allowed the day-to-day variability of model parameters to be detected under both well-watered and soil drying conditions, thus providing more accurate parameter estimates and model simulations compared to a larger window size (Steppe et al., 2008). A sensitivity analysis of the model revealed the identifiable parameters (according to De Pauw et al., 2008a, 2008b) that can be unambiguously estimated during model calibration from the available measurements: the hydraulic capacitance of the water storage tissue in the stem compartment, the xylem

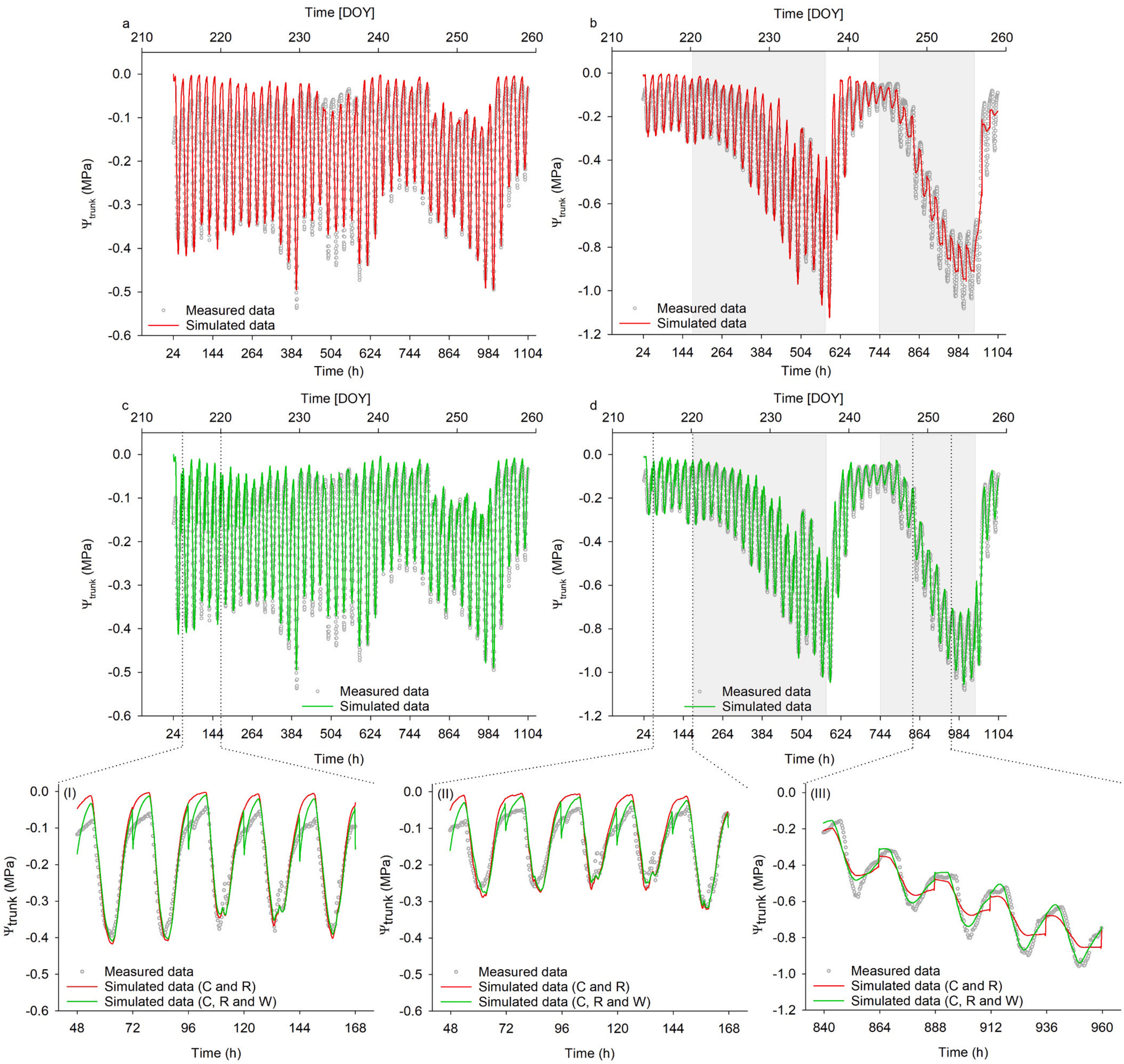

Fig. 5. Comparison between measured (dots) and simulated (lines) ψ_{trunk} using two calibration methods: i) hydraulic capacitance of the water storage tissue in the stem compartment (C) and xylem hydraulic resistance in the soil-to-stem segment (R) as calibrated parameters and ii) C, R and initial amount of water stored in the stem compartment (W) as calibrated parameters in the (a, c) well-watered and (b, d) drought irrigation treatments. Panels (I-III) illustrate specific differences between the model outputs obtained with the two types of calibration. The grey bands indicate the periods of reduced irrigation that led to the development of drought stress.

hydraulic resistance in the soil-to-stem segment, and the initial amount of water stored in the stem compartment. Based on the results of the identifiability analysis, a first attempt was made to calibrate two identifiable parameters (C and R) on both well-watered and drought datasets. The model showed a good fit to the measured trunk water potential data in the well-watered dataset (Fig. 5a), but was unable to adequately describe the drought dataset, particularly in the second drought phase (Fig. 5b). When three identifiable parameters were calibrated on both well-watered and drought datasets, the model was able to accurately describe the steeper decline in trunk water potential (Fig. 5d) due to more severe soil drying (Fig. 4b). The inclusion of the third identifiable parameter in the calibration process had negligible effects on the calibrated parameters (C and R) for the well-watered (Fig. 8a, b) and much of the drought (Fig. 8c, d) datasets. However, during the severe drought phase, these differences became evident, with the calibration of the initial value of stored water also improving the other calibrated variables. The inclusion of initial stored water (W) in the calibration process allowed this parameter to be adapted daily during the moving window calibration, rather than relying on a fixed initial value and subsequent calculated state values of W at the start of each window (Fig. 9). Although a fixed initial value was adequate to allow the model to describe the behavior of kiwifruit vines under well-watered conditions (Fig. 9a), the initial stored water reached unrealistic values in the second, more severe drought phase (Fig. 9b). This suggests that the initial value of stored water should be included as a calibration variable when there is a rapid drop in trunk water potential (i.e., during severe drought

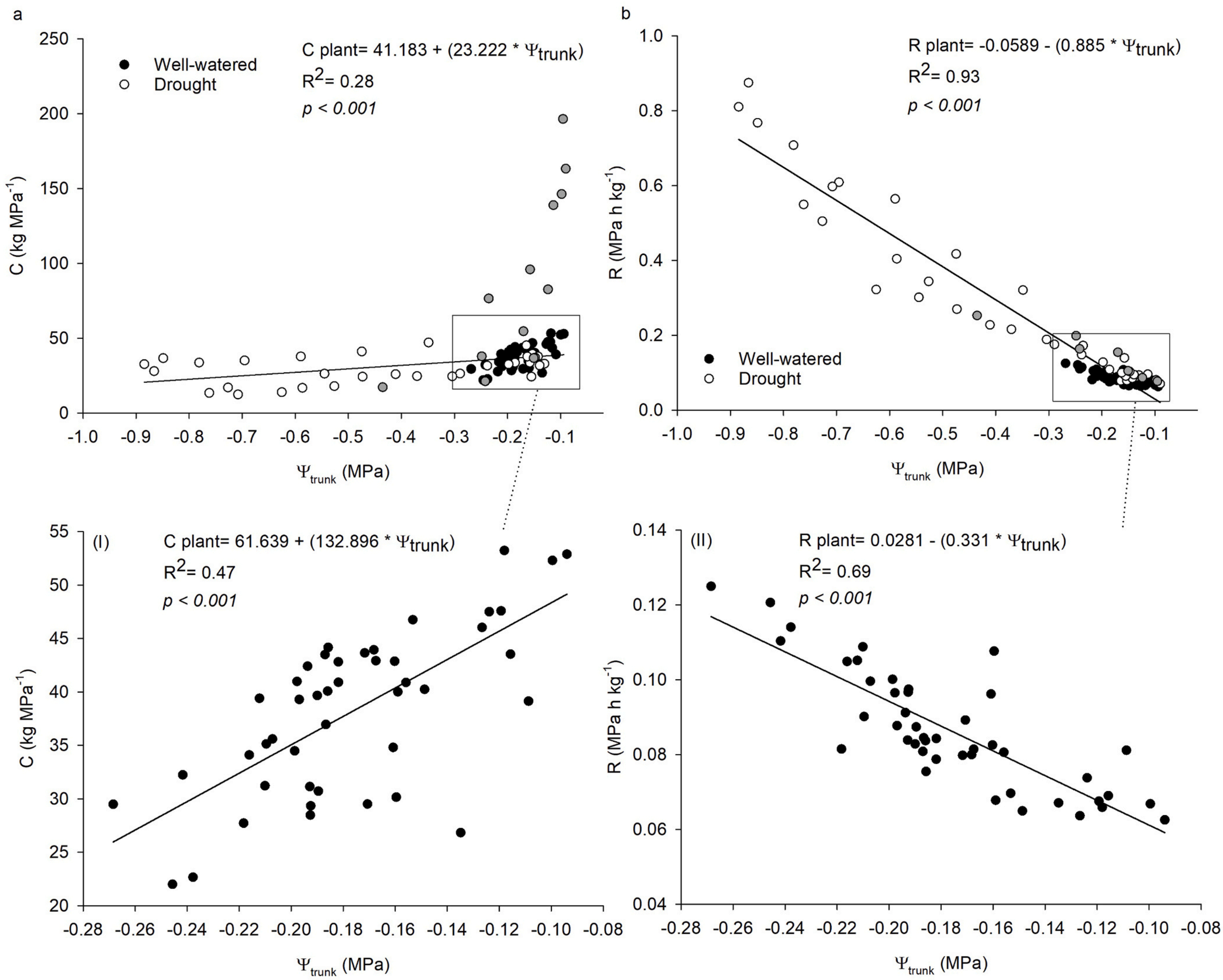

Fig. 6. Daily values of (a) hydraulic capacitance of the water storage tissue in the stem compartment (C) and (b) xylem hydraulic resistance in the soil-to-stem segment (R) as a function of daily average trunk water potential (ψ_{trunk}) in both well-watered and drought irrigation treatments. Model calibration was performed with all three parameters (C, R and initial amount of water stored in the stem compartment, W). Grey points indicate the values of the drought treatment as affected by re-watering. Panels I-II illustrate the relationship of C and R with daily average ψ_{trunk} in the well-watered irrigation treatment.

stress). The results of this study clearly show the importance and advantages of performing an identifiability analysis, which improves the model to better describe the experimental data, especially under drought stress conditions, according to De Pauw et al. (2008a). Indeed, in the present study it was advisable to include the initial amount of water stored in the stem compartment as a calibration parameter, especially during the more severe drought stress, as it improved the simulation of trunk water potential and enabled improved estimates of key hydraulic parameters to describe the response of kiwifruit vines to drought. Contrarily, a variable initial W value may not improve model performance under well-watered conditions as C and R are expected to remain almost constant. The adapted model for continuous modelling of kiwifruit vine water status and hydraulic behavior was then successfully applied under conditions ranging from wet to more or less severe drought.

4.2. Modelling vine drought response

The study of plant hydraulics is of increasing interest to better understand the impacts of drought and to predict how plants will respond to climate change (Sperry and Love, 2015; De Swaef et al., 2022; Torres-Ruiz et al., 2024). Mechanistic plant models, in combination with plant measurements, represent promising tools to increase knowledge on various plant physiological processes and hydraulic functioning (Steppe et al., 2015b; De Swaef et al., 2022), showing great potential for understanding the effects of limiting soil water availability and the hydraulic response of plants to drought (Baert et al., 2015; Salomón et al., 2017). The nature of hydraulic constraints on plant functioning is increasingly being addressed (Williams et al., 2001), and several variants of plant hydraulic models have been proposed over the last two decades (Paschalis et al., 2024).

In particular, the study of tissue hydraulic capacitance and storage capacity and their inclusion in models has received increasing attention due to the dynamic nature of water transport throughout the plant (Steppe et al., 2015b). A key parameter widely included in most models is hydraulic resistance in the soil-to-plant segment, as it greatly influences plant water status and responses to drought (Baert et al., 2015). Therefore, one of the objectives of our study was to use an effective model to derive key hydraulic parameters, such as hydraulic capacitance and resistance, that are otherwise difficult to measure and that can help characterize the drought responses and mechanisms of kiwifruit vines. Our model was adapted from Steppe et al. (2006); (2008) and simplified

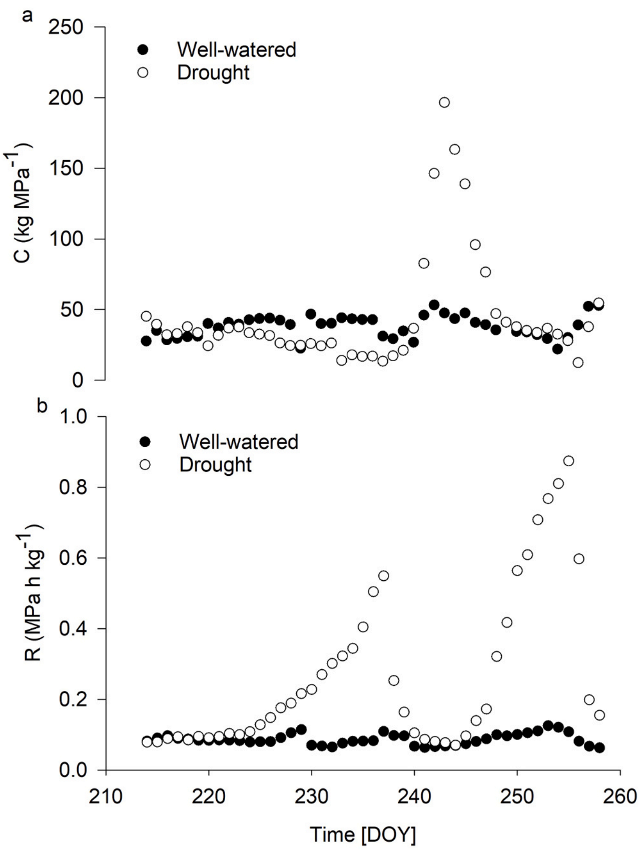

Fig. 7. Time evolution of the daily calibrated model parameter values during the irrigation experiment in both well-watered and drought-stressed kiwifruit vines: (a) hydraulic capacitance of the water storage tissue in the stem compartment (C); (b) xylem hydraulic resistance in the soil-to-stem segment (R). Time is expressed in day of the year [DOY].

to describe only the processes occurring in the stem compartment, with a water flow resistance (R) and accounting for water storage in the stem by including plant hydraulic capacitance (C) (Fig. 2). Although most models do not account for drought-induced C variability, the dynamic nature of C should be considered in mechanistic water transport models to better understand the hydraulic functioning of plants (Salomón et al., 2017). Woody plants absorb water, store it at night in several compartments and release it during the day for leaf transpiration, representing an important mechanism to regulate the dynamics of transpiration (Gao et al., 2021). Hydraulic capacitance reflects the ability of a tissue to store and release water into the xylem in response to a given change in tissue water potential (Steppe et al., 2006; Scholz et al., 2007, 2011; Meinzer et al., 2010). Capacitive water release into the transpiration stream can buffer daily fluctuations in xylem tension by reducing or slowing down transpiration-induced xylem pressure drops (Meinzer et al., 2009; McCulloh et al., 2014; Epila et al., 2017; Steppe, 2018), thereby reducing the risk of xylem embolism and hydraulic failure under dynamic conditions (Scholz et al., 2011). Instead, R represents the resistance to water flow and has been shown to vary between species, in part due to differences in xylem vessels structure and size (Tyree and Ewers, 1991; Sperry et al., 2006), and the model-derived parameter has previously been linked to a realistic wood anatomical basis (Steppe and Lemeur, 2007).

The hydraulic parameters of yellow-fleshed kiwifruit vines under Mediterranean field conditions have been poorly studied, and this is the first study to use a mechanistic plant water flow model to unravel kiwifruit drought behavior. Model calibrations and outputs from this study revealed that hydraulic parameters such as C and R fell within realistic ranges and highlighted important changes in the hydraulic behavior of well-watered and drought-stressed kiwifruit vines (Fig. 6). In particular, the C values obtained in our study ranged from 22 to 53 kg MPa^{-1} for the well-watered vines, while in the drought-stressed vines C progressively decreased during the drought periods, reaching lower values of about 12 kg MPa^{-1} (Fig. 7a). Instead, the R values ranged from 0.062 to 0.12 MPa h kg^{-1} for the well-watered vines, while in the drought-stressed vines R progressively increased during the drought periods, reaching higher values of about 0.87 MPa h kg^{-1} (Fig. 7b). Data on C are now available for several species from a variety of ecosystems, with different architectures (stem diameter and tree size), wood types and densities, but comparison with values in the literature is not straightforward due to inconsistent use of capacitance units (Scholz et al., 2011). A wide range of published values of R can also be found in different units (Verbeeck et al., 2007). Calibrated values for C were found to range from 23.7 to 69 kg MPa^{-1} for Scots pine (Verbeeck et al., 2007), and approximately 212 and 940 mg MPa^{-1} for beech and oak trees, respectively (Steppe and Lemeur, 2007). Calibrated values for R were found to range from 0.46 to 1 MPa h kg^{-1} for Scots pine (Verbeeck et al., 2007), and approximately 0.18 and 0.11 MPa s mg^{-1} for beech and oak trees, respectively (Steppe and Lemeur, 2007).

The linear relationships between ψ_{trunk} and C and R strongly confirm that variations in plant hydraulic properties are strictly related to variations in plant water relations and status (Torres-Ruiz et al., 2024). In particular, C was found to decrease with more negative ψ_{trunk} values (Fig. 6a), whereas R showed an increase (Fig. 6b). These results align with previous studies on various woody species that have examined changes in C and R across a gradient of plant water potential. These studies consistently report that C decreases and R increases with more negative plant water potential values, supported by strong correlations (Meinzer et al., 2003, 2009; Scholz et al., 2007; Salomón et al., 2017). A previous study on pot-grown kiwifruit vines (cv. 'Hayward') found that the water released to the transpiration stream from different tissues (leaves, shoots, branches, roots and fruits) corresponded to 8.5 % of total transpiration (measured from pre-dawn to 2 p.m.) for control vines, 9.6 % for moderately stressed vines and 5.1 % for vines with the least water available (Nuzzo et al., 1997). These values are relatively low compared to other fruit trees, such as olive trees, whose leaves can use about 60 % of their water reserves for transpiration without irreversible damage (Sofo et al., 2008). In addition, the high root/canopy ratio and the efficiency of the vascular system allow kiwifruit vines to satisfy approximately 91 % of their transpiration demand directly through root water uptake from the soil, under non-limiting soil water availability conditions (Nuzzo et al., 1997). The model-derived capacitance values, which showed a progressive decrease with increasing drought stress, are consistent with the observed tendency of kiwifruit vines to reduce the release of stored water into the transpiration stream under drought stress. Instead, hydraulic resistance was found to significantly increase under persistent drought conditions in woody trees and grapevines (Baert et al., 2015; Peters et al., 2021). As soil water content decreases, hydraulic resistance to water flow in the soil increases and soil matric potential decreases, resulting in steeper water potential gradients within the plant (i.e. more negative plant water potential values) (Scharwies and Dinneny, 2019). Large xylem vessels, reported to be between 0.12 and 0.5 mm in both root and stem of kiwifruit, provide a very low resistance pathway for water movement within the vine (McAneney and Judd, 1983), but at the same time could contribute to a more frequent occurrence of embolism formation, even at relatively high xylem water potential values (Clearwater and Clark, 2003). The increase in R, which has been found to increase as the soil dries (McAneney and Judd, 1983), may also be driven by physical changes in the xylem, such as embolism formation resulting from drought stress. The C and R parameters derived through model simulation and calibration allowed further characterization of the hydraulic behavior of yellow-fleshed kiwifruit vines under different irrigation conditions. This understanding is particularly valuable in semi-arid Mediterranean environments, where optimized water management is increasingly critical.

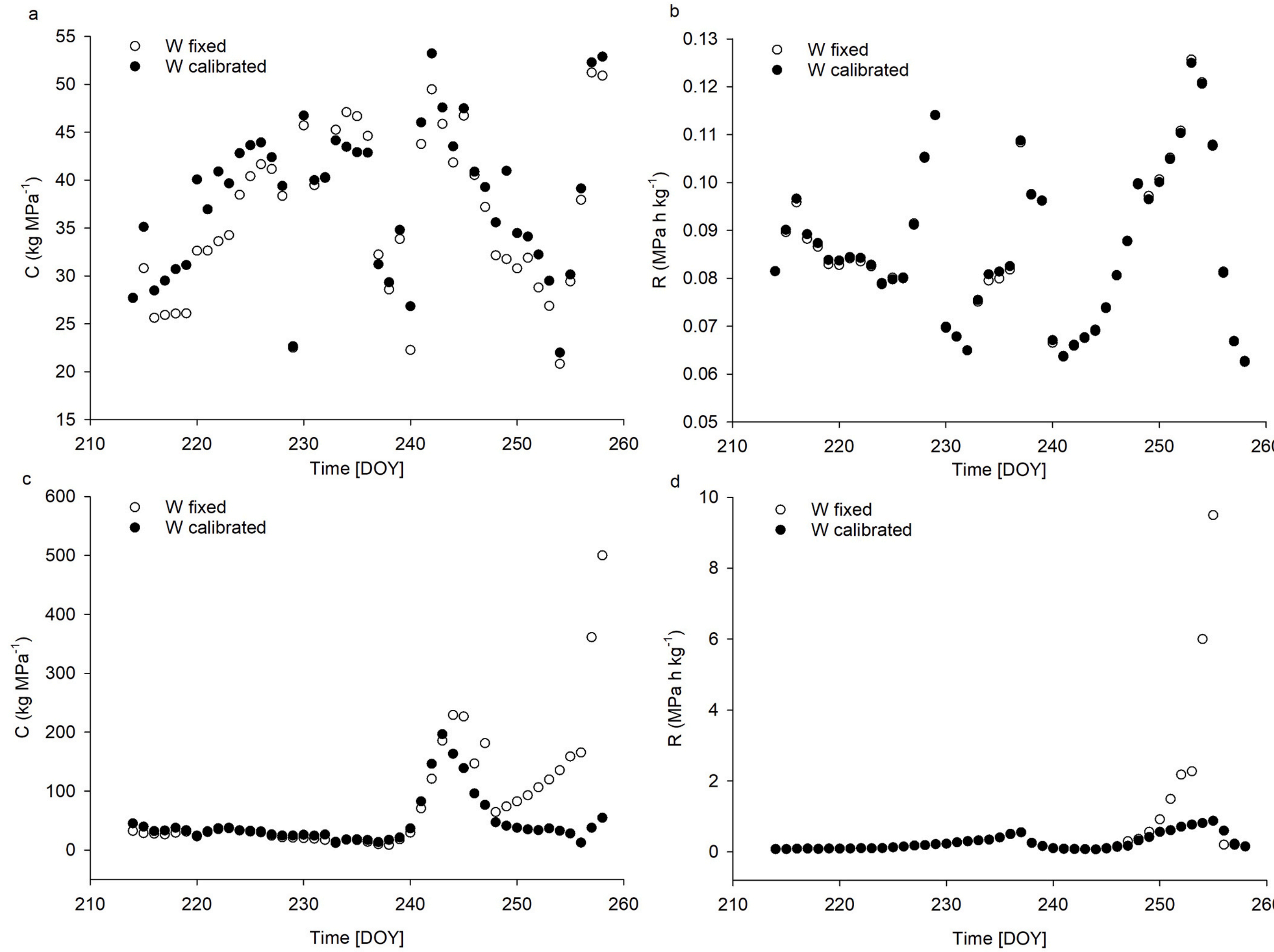

Fig. 8. Comparison of daily calibrated model parameter values (hydraulic capacitance of the water storage tissue in the stem compartment, C, and xylem hydraulic resistance in the soil-to-stem segment, R) obtained from model calibration with adaptation of two (C and R) or three (C, R and initial amount of water stored in the stem compartment, W) parameters during the irrigation experiment in (a, b) well-watered and (c, d) drought irrigation treatments. Time is expressed in day of the year [DOY].

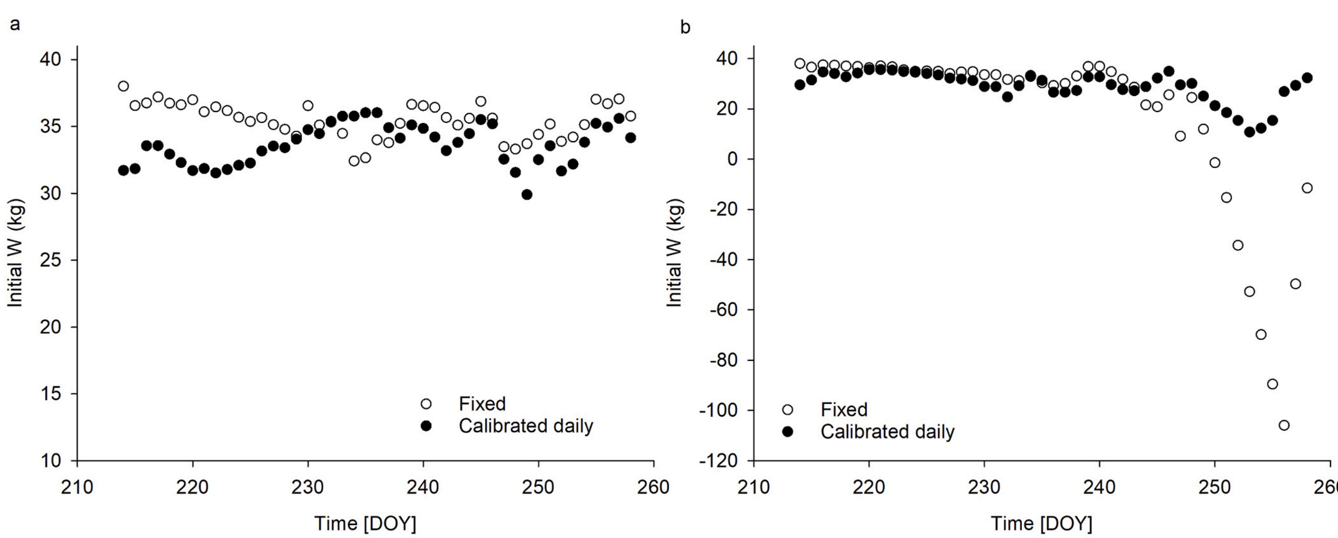

Fig. 9. Comparison of initial values of stored water (W) using two model calibration approaches: one where the initial value of W was fixed at the value obtained from the end of the previous 1-day moving window and only two parameters (C and R) were calibrated, and another where the initial value of W, alongside with C and R, was recalibrated daily in the (a) well-watered and the (b) drought irrigation treatment. Time is expressed in day of the year [DOY].

4.3. Potential use of mechanistic models for irrigation

In addition to advancing our understanding of the hydraulic functioning of kiwifruit vines and the dynamics of water transport, the modelling process can be integrated into a practical automated monitoring system. This approach enables the development of a tool for real-world irrigation applications, as previously demonstrated by Steppe et al. (2008). Plant measurements, based on sap flow and trunk water potential, are fed into a mechanistic plant model, to continuously derive key hydraulic parameters that can be used as promising indicators to detect drought stress conditions and thus guide irrigation decisions. Our drought stress experiment shows that measured ψ_{trunk} deviated from the expected pattern (well-watered vines) once drought stress was imposed by modulating irrigation (Fig. 5). Integrating these measurements with sap flow data and mechanistic plant modelling enables the daily derivation of plant hydraulic parameters that are otherwise challenging to measure. In addition, as the measurements from the plant sensors are continuous, the hydraulic functioning of vines or fruit trees can be modelled continuously, rather than being limited to discrete observations, contributing to the study of the hydraulic functioning of plants under natural conditions throughout the growing season. These hydraulic parameters have been shown to strongly correlate with plant water status, providing a unique and valuable perspective on plant behavior under varying water conditions. However, the relationship between C and R with ψ_{trunk} was also observed under well-watered conditions, demonstrating that the calibrated parameters changed within a narrow range of plant water potential (e.g., ψ_{trunk} ranged from approximately −0.1 MPa to −0.3 MPa under well-watered conditions). This highlights their sensitivity and underscores their strong correlation with the water status of the vines (Fig. 6, panels I-II). The investigated variations and dynamics of C and R of yellow-fleshed kiwifruit vines in relation to plant water status highlight the potential of these parameters to be used as indicators of drought stress and for irrigation purposes, the opportunities of which should be further explored. The modelling approach developed can be effectively tested and transferred to various fruit crops, providing the basis for future research to implement practical tools that can be used in real-world irrigation applications.

5. Conclusions

As drought events are expected to increase in the coming years, especially in the Mediterranean area, it is important to gain knowledge on the drought response and hydraulic behavior of crops under field conditions. This study combines plant sensor measurements with a mechanistic water transport model to enable real-time, *in-situ* field monitoring of hydraulic capacitance and resistance, revealing the drought response of kiwifruit vines. In particular, the kiwifruit trunk water potential model showed a progressive decrease in the hydraulic capacitance and a substantial increase in the hydraulic resistance with increasing soil and plant water deficit. To date, several models have been developed to gain a better understanding of the plant processes related to drought stress. However, since sensors are still not cost-effective and taking measurements at farm level is challenging, modelling approaches have tended to remain within the scientific and research communities rather than being used by farmers. We strongly believe that sensor technologies will be increasingly adopted over the next few years, leading to a new generation of irrigation decision tools that use plant monitoring and mathematical plant modelling to inform irrigation. Within this framework, the used model not only introduces relevant information on the hydraulic functioning of kiwifruit vines in response to drought stress in a Mediterranean environment, but also shows great potential as a basis for developing real-time, plant-based irrigation management that can be transferred to various fruit crops.

6. Funding

This paper reports on parts of the Ph.D. study undertaken by MC at the Laboratory of Plant Ecology of Ghent University. The authors thank the 'Instituto Nazionale Previdenza Sociale' (INPS) for providing the Ph. D. funding. This study has been partially supported by the Italian Ministry of University and Research (MUR) in the frame of the PON "RICERCA E INNOVAZIONE" 2014–2020 Project RESO "Sistemi di coltivazione resilienti, valutazione di impatto delle produzioni frutticole", AGRIFOOD CUP B34I200000320005. This publication is based upon work conducted within and interactions facilitated by COST Action CA21142 FruitCREWS, supported by COST (European Cooperation in Science and Technology).

CRediT authorship contribution statement

Maria Calabritto: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Alba N. Mininni:** Investigation, Project administration, Supervision, Writing – review & editing. **Dirk J.W. De Pauw:** Data curation, Methodology, Software, Supervision, Writing – review & editing. **Steve Green:** Data curation, Supervision, Writing – review & editing. **Bartolomeo Dichio:** Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing. **Kathy Steppe:** Conceptualization, Formal analysis, Investigation, Methodology, Resources, 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.

Data availability

Data will be made available on request.

References

Allen, R.G., Pereira, L.S., Raes, D., Smith, M., 1998. Crop evapotranspiration: guidelines for computing crop water requirements. Food Agric. Organ. U. Nations Irrig. Drain. Pap. 56. ⟨https://www.fao.org/4/x0490e/x0490e00.htm⟩ (Rome, Italy).
Baert, A., De Schepper, V., Steppe, K., 2015. Variable hydraulic resistances and their impact on plant drought response modelling. Tree Physiol. 35 (4), 439–449. https://doi.org/10.1093/treephys/tpu078.
Brahmanand, P.S., Singh, A.K., 2022. Precision irrigation water management-current status, scope and challenges. Ind. J. Fertil. 18, 372–380.
Bwambale, E., Abagale, F.K., Anornu, G.K., 2022. Smart irrigation monitoring and control strategies for improving water use efficiency in precision agriculture: a review. Agric. Water Manag. 260, 107324. https://doi.org/10.1016/j.agwat.2021.107324.
Calabritto, M., Mininni, A.N., Di Biase, R., Pietrafesa, A., Dichio, B., 2024. Spatio-temporal dynamics of root water uptake and identification of soil moisture thresholds for precision irrigation in a Mediterranean yellow-fleshed kiwifruit orchard. Front. Plant Sci. 15, 1472093. https://doi.org/10.3389/fpls.2024.1472093.
Calderón-Orellana, A., Silva, D.I., Bastías, R.M., Bambach, N., Aburto, F., 2021. Late-season plastic covering delays the occurrence of severe water stress and improves intrinsic water use efficiency and fruit quality in kiwifruit vines. Agric. Water Manag. 249, 106795. https://doi.org/10.1016/j.agwat.2021.106795.
Chartzoulakis, K., Noitsakis, B., Therios, I., 1993. Photosynthesis, plant growth and dry matter distribution in kiwifruit as influenced by water deficits. Irrig. Sci. 14, 1–5. https://doi.org/10.1007/BF00194999.
Clearwater, M.J., Clark, C.J., 2003. In vivo magnetic resonance imaging of xylem vessel contents in woody lianas. Plant Cell Environ. 26 (8), 1205–1214. https://doi.org/10.1046/j.1365-3040.2003.01042.x.
Cohen, Y., Fuchs, M., Green, G.C., 1981. Improvement of the heat pulse method for determining sap flow in trees. Plant Cell Environ. 4 (5), 391–397. https://doi.org/10.1111/j.1365-3040.1981.tb02117.x.
Condon, J.M., 1992. Aspects of kiwifruit stem structure in relation to transport. Acta Hortic. 297, 419–426. https://doi.org/10.17660/ActaHortic.1992.297.55.
Da Sois, L., Mencuccini, M., Castells, E., Sanchez-Martinez, P., Martínez-Vilalta, J., 2024. How are physiological responses to drought modulated by water relations and leaf economics' traits in woody plants? Agric. Water Manag 291, 108613. https://doi.org/10.1016/j.agwat.2023.108613.

Dastane, N.G., 1974. Effective rainfall in irrigated agriculture. Food Agric. Organ. U. Nations Irrig. Drain. Pap. 25. ⟨https://www.fao.org/4/x5560e/x5560e00.htm⟩ (Rome, Italy).
De Pauw, D.J.W., Steppe, K., De Baets, B., 2008a. Identifiability analysis and improvement of a tree water flow and storage model. Math. Biosci. 211 (2), 314–332. https://doi.org/10.1016/j.mbs.2007.08.007.
De Pauw, D.J., Steppe, K., De Baets, B., 2008b. Unravelling the output uncertainty of a tree water flow and storage model using several global sensitivity analysis methods. Biosyst. Eng. 101 (1), 87–99. https://doi.org/10.1016/j.biosystemseng.2008.05.011.
De Swaef, T., Pieters, O., Appeltans, S., Borra-Serrano, I., Coudron, W., Couvreur, V., Garré, S., Lootens, P., Nicolaï, P., Pols, L., Saint Cast, C., Šalagovič, J., Van Haeverbeke, M., Stock, M., Wyffels, F., 2022. On the pivotal role of water potential to model plant physiological processes. Silico Plants 4 (1), 1–28. https://doi.org/10.1093/insilicoplants/diab038.
Dichio, B., Montanaro, G., Sofo, A., Xiloyannis, C., 2013. Stem and whole-plant hydraulics in olive (*olea europaea*) and kiwifruit (*actinidia deliciosa*). Trees 27, 183–191. https://doi.org/10.1007/s00468-012-0787-3.
Epila, J., De Baerdemaeker, N.J.F., Vergeynst, L.L., Maes, W.H., Beeckman, H., Steppe, K., 2017. Capacitive water release and internal leaf water relocation delay drought-induced cavitation in African *maesopsis eminii*. Tree Physiol. 37, 481–490. https://doi.org/10.1093/treephys/tpw128.
Fereres, E., Evans, R.G., 2006. Irrigation of fruit trees and vines: an introduction. Irrig. Sci. 24, 55–57. https://doi.org/10.1007/s00271-005-0019-3.
Ferguson, A.R., 1984. Kiwifruit: a botanical review. In: Janick, J. (Ed.), Horticultural reviews. Avi Publishing Company, Inc., Connecticut, pp. 1–64.
Gao, Z., Fan, J., Li, Z., 2021. Dynamic simulation water storage of different parts in peach tree under drought stress. Agric. Water Manag. 244, 106537. https://doi.org/10.1016/j.agwat.2020.106537.
Genard, M., Fishman, S., Vercambre, G., Huguet, J.G., Bussi, C., Besset, J., Habib, R., 2001. A biophysical analysis of stem and root diameter variations in woody plants. Plant Physiol. 126 (1), 188–202. https://doi.org/10.1104/pp.126.1.188.
van Genuchten, M.T., 1980. A closed-form equation for predicting the hydraulic conductivity of unsaturated soils. Soil Sci. Soc. Am. J. 49, 12–19. https://doi.org/10.2136/sssaj1980.03615995004400050002x.
Goldhamer, D.A., Fereres, E., Mata, M., Girona, J., Cohen, M., 1999. Sensitivity of continuous and discrete plant and soil water status monitoring in peach trees subjected to deficit irrigation. J. Am. Soc. Hortic. Sci. 124 (4), 437–444. https://doi.org/10.21273/JASHS.124.4.437.
Goudriaan, J., van Laar, H.H., 1994. Modelling Potential Crop Growth Processes, first ed. Kluwer Academic Publishers, Dordrecht. https://doi.org/10.1007/978-94-011-0750-1.
Green, S., Clothier, B., Jardine, B., 2003. Theory and practical application of heat pulse to measure sap flow. Agron. J. 95 (6), 1371–1379. https://doi.org/10.2134/agronj2003.1371.
Green, S.R., McNaughton, K.G., Clothier, B.E., 1989. Observations of night-time water use in kiwifruit vines and apple trees. Agric. For. Meteor. 48 (3-4), 251–261. https://doi.org/10.1016/0168-1923(89)90072-5.
Green, S., Reyes, F., Dichio, B., Mastroleo, M., Xylogiannis, E., 2022. Water use of yellow-fleshed kiwifruit during an annual cycle. Acta Hortic. (1332), 187–194. https://doi.org/10.17660/ActaHortic.2022.1332.25.
Gucci, R., Massai, R., Xiloyannis, C., Flore, J.A., 1996. The effect of drought and vapour pressure deficit on gas exchange of young kiwifruit (*actinidia deliciosa* var. *deliciosa*) vines. Ann. Bot. 77 (6), 605–613. https://doi.org/10.1006/anbo.1996.0076.
Holzapfel, E.A., Merino, R., Mariño, M.A., Matta, R., 2000. Water production functions in kiwi. Irrig. Sci. 19, 73–79. https://doi.org/10.1007/s002710050003.
Intrigliolo, D.S., Castel, J.R., 2004. Continuous measurement of plant and soil water status for irrigation scheduling in plum. Irrig. Sci. 23, 93–102. https://doi.org/10.1007/s00271-004-0097-7.
Judd, M.J., McAneney, K.J., Wilson, K.S., 1989. Influence of water stress on kiwifruit growth. Irrig. Sci. 10, 303–311. https://doi.org/10.1007/BF00257495.
Lionello, P., Scarascia, L., 2018. The relation between climate change in the Mediterranean region and global warming. Reg. Environ. Change 18, 1481–1493. https://doi.org/10.1007/s10113-018-1290-1.
McAneney, K.J., Judd, M.J., 1983. Observations on kiwifruit (*actinidia chinensis* Planch.) root exploration, root pressure, hydraulic conductivity, and water uptake. N. Zeal J. Agr. Res. 26 (4), 507–510. https://doi.org/10.1080/00288233.1983.10427029.
McCulloh, K.A., Johnson, D.M., Meinzer, F.C., Woodruff, D.R., 2014. The dynamic pipeline: hydraulic capacitance and xylem hydraulic safety in four tall conifer species. Plant Cell Environ. 37 (5), 1171–1183. https://doi.org/10.1111/pce.12225.
McCutchan, H., Shackel, K.A., 1992. Stem-water potential as a sensitive indicator of water stress in prune trees (*prunus domestica* L. cv. French). J. Am. Soc. Hortic. Sci. 117, 607–611.
Meinzer, F.C., James, S.A., Goldstein, G., Woodruff, D., 2003. Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees. Plant Cell Environ. 26 (7), 1147–1155. https://doi.org/10.1046/j.1365-3040.2003.01039.x.
Meinzer, F.C., Johnson, D.M., Lachenbruch, B., McCulloh, K.A., Woodruff, D.R., 2009. Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. Funct. Ecol. 23 (5), 922–930. https://doi.org/10.1111/j.1365-2435.2009.01577.x.
Meinzer, F.C., McCulloh, K.A., Lachenbruch, B., Woodruff, D.R., Johnson, D.M., 2010. The blind men and the elephant: the impact of context and scale in evaluating conflicts between plant hydraulic safety and efficiency. Oecologia 164, 287–296. https://doi.org/10.1007/s00442-010-1734-x.
Milano, M., Ruelland, D., Fernandez, S., Dezetter, A., Fabre, J., Servat, E., Fritsch, J.M., Ardoin-Bardin, S., Thivet, G., 2013. Current state of Mediterranean water resources and future trends under climatic and anthropogenic changes. Hydrol. Sci. J. 58 (3), 498–518. https://doi.org/10.1080/02626667.2013.774458.
Mills, T.M., Li, J., Behboudian, M.H., 2009. Physiological responses of gold kiwifruit (*actinidia chinensis*) to reduced irrigation. J. Am. Soc. Hortic. Sci. 134 (6), 677–683. https://doi.org/10.21273/JASHS.134.6.677.
Mininni, A.N., Laterza, D., Tuzio, A.C., Di Biase, R., Dichio, B., 2022. Soil water content monitoring as a tool for sustainable irrigation strategy in a kiwifruit orchard under semi-arid conditions. Acta Hortic. 1332, 203–210. https://doi.org/10.17660/ActaHortic.2022.1332.27.
Montanaro, G., Dichio, B., Xiloyannis, C., 2007. Response of photosynthetic machinery of field-grown kiwifruit under Mediterranean conditions during drought and re-watering. Photosynthetica 45, 533–540. https://doi.org/10.1007/s11099-007-0091-4.
Montanaro, G., Dichio, B., Xiloyannis, C., 2009. Shade mitigates photoinhibition and enhances water use efficiency in kiwifruit under drought. Photosynthetica 47, 363–371. https://doi.org/10.1007/s11099-009-0057-9.
Moriana, A., Pérez-López, D., Prieto, M.H., Ramírez-Santa-Pau, M., Pérez-Rodriguez, J. M., 2012. Midday stem water potential as a useful tool for estimating irrigation requirements in olive trees. Agric. Water Manag. 112, 43–54. https://doi.org/10.1016/j.agwat.2012.06.003.
Mualem, Y., 1976. A new model for predicting the hydraulic conductivity of unsaturated porous media. Water Resour. Res. 12, 513–522. https://doi.org/10.1029/WR012i003p00513.
Noun, G., Lo Cascio, M., Spano, D., Marras, S., Sirca, C., 2022. Plant-based methodologies and approaches for estimating plant water status of Mediterranean tree species: a semi-systematic review. Agronomy 12 (9), 2127. https://doi.org/10.3390/agronomy12092127.
Nuzzo, V., Dichio, B., Xiloyannis, C., Piccotino, D., Massai, R., 1997. Contribution to transpiration of different tissues of kiwifruit vines from their water reserves. Acta Hortic. 444, 329–334. https://doi.org/10.17660/ActaHortic.1997.444.51.
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., Casadesus, J., Bonany, J., Torrecillas, A., 2010. Could trunk diameter sensors be used in woody crops for irrigation scheduling? A review of current knowledge and future perspectives. Agric. Water Manag. 97, 1–11. https://doi.org/10.1016/j.agwat.2009.09.008.
Pagay, V., 2022. Evaluating a novel microtensiometer for continuous trunk water potential measurements in field-grown irrigated grapevines. Irrig. Sci. 40 (1), 45–54. https://doi.org/10.1007/s00271-021-00758-8.
Paschalis, A., De Kauwe, M.G., Sabot, M., Fatichi, S., 2024. When do plant hydraulics matter in terrestrial biosphere modelling? Glob. Change Biol. 30 (1), e17022. https://doi.org/10.1111/gcb.17022.
Peters, R.L., Steppe, K., Cuny, H.E., De Pauw, D.J., Frank, D.C., Schaub, M., Rathgeber, C. B.K., Cabon, A., Fonti, P., 2021. Turgor–a limiting factor for radial growth in mature conifers along an elevational gradient. N. Phytol. 229 (1), 213–229. https://doi.org/10.1111/nph.16872.
Prada, J., Dinis, L.T., Soriato, E., Vandelle, E., Soletkin, O., Uysal, Ş., Dihazi, A., Santos, C., Santos, J.A., 2024. Climate change impact on Mediterranean viticultural regions and site-specific climate risk-reduction strategies. Mitig. Adapt. Strateg. Glob. Chang 29 (6), 1–43. https://doi.org/10.1007/s11027-024-10146-0.
Rajan, P., Natraj, P., Kim, M., Lee, M., Jang, Y.J., Lee, Y.J., Kim, S.C., 2024. Climate change impacts on and response strategies for kiwifruit production: a comprehensive review. Plants 13 (17), 2354. https://doi.org/10.3390/plants13172354.
Richards, L.A., 1948. Porous plate apparatus for measuring moisture retention and transmission by soil. Soil Sci. 66 (2), 105–110. https://doi.org/10.1097/00010694-194808000-00003.
Salomón, R.L., Limousin, J.M., Ourcival, J.M., Rodríguez-Calcerrada, J., Steppe, K., 2017. Stem hydraulic capacitance decreases with drought stress: implications for modelling tree hydraulics in the Mediterranean oak *quercus ilex*. Plant Cell Environ. 40 (8), 1379–1391. https://doi.org/10.1111/pce.12928.
Scharwies, J.D., Dinneny, J.R., 2019. Water transport, perception, and response in plants. J. Plant Res. 132 (3), 311–324. https://doi.org/10.1007/s10265-019-01089-8.
Scholz, F.G., Bucci, S.J., Goldstein, G., Meinzer, F.C., Franco, A.C., Miralles-Wilhelm, F., 2007. Biophysical properties and functional significance of stem water storage tissues in neotropical savanna trees. Plant Cell Environ. 30 (2), 236–248. https://doi.org/10.1111/j.1365-3040.2006.01623.x.
Scholz, F.G., Phillips, N.G., Bucci, S.J., Meinzer, F.C., Goldstein, G., 2011. Hydraulic capacitance: biophysics and functional significance of internal water sources in relation to tree size. In: Meinzer, F.C., Lachenbruch, B., Dawson, T.E. (Eds.), Size-and age-related changes in tree structure and function. Springer Dordrecht Publishing, Netherlands, pp. 341–361.
Seager, R., Osborn, T.J., Kushnir, Y., Simpson, I.R., Nakamura, J., Liu, H., 2019. Climate variability and change of Mediterranean-type climates. J. Clim. 32 (10), 2887–2915. https://doi.org/10.1175/JCLI-D-18-0472.1.
Shackel, K., 2011. A plant-based approach to deficit irrigation in trees and vines. HortScience 46 (2), 173–177. https://doi.org/10.21273/HORTSCI.46.2.173.
Soares, D., Paço, T.A., Rolim, J., 2022. Assessing climate change impacts on irrigation water requirements under Mediterranean conditions—a review of the methodological approaches focusing on maize crop. Agronomy 13 (1), 117. https://doi.org/10.3390/agronomy13010117.
Sofo, A., Manfreda, S., Fiorentino, M., Dichio, B., Xiloyannis, C., 2008. The olive tree: a paradigm for drought tolerance in Mediterranean climates. Hydrol. Earth Syst. Sci. 12 (1), 293–301. https://doi.org/10.5194/hess-12-293-2008.

Sperry, J.S., Hacke, U.G., Pittermann, J., 2006. Size and function in conifer tracheids and angiosperm vessels. Am. J. Bot. 93 (10), 1490–1500. https://doi.org/10.3732/ajb.93.10.1490.

Sperry, J.S., Love, D.M., 2015. What plant hydraulics can tell us about responses to climate-change droughts. N. Phytol. 207 (1), 14–27. https://doi.org/10.1111/nph.13354.

Steduto, P., Hsiao, T.C., Fereres, E., Raes, D., 2012. Crop yield response to water. Food Agric. Organ. U. Nations Irrig. Drain. Pap. 66. ⟨https://www.fao.org/4/i2800e/i2800e00.htm⟩ (Rome, Italy).

Steppe, K., 2013. Water ascends in woody plants: so what? Acta Hortic. 990, 305–311. https://doi.org/10.17660/ActaHortic.2013.990.36.

Steppe, K., 2018. The potential of the tree water potential. Tree Physiol. 38, 937–940. https://doi.org/10.1093/treephys/tpy064.

Steppe, K., De Pauw, D.J., Lemeur, R., 2008. A step towards new irrigation scheduling strategies using plant-based measurements and mathematical modelling. Irrig. Sci. 26, 505–517. https://doi.org/10.1007/s00271-008-0111-6.

Steppe, K., De Pauw, D.J., Lemeur, R., Vanrolleghem, P.A., 2006. A mathematical model linking tree sap flow dynamics to daily stem diameter fluctuations and radial stem growth. Tree Physiol. 26 (3), 257–273. https://doi.org/10.1093/treephys/26.3.257.

Steppe, K., Lemeur, R., 2007. Effects of ring-porous and diffuse-porous stem wood anatomy on the hydraulic parameters used in a water flow and storage model. Tree Physiol. 27 (1), 43–52. https://doi.org/10.1093/treephys/27.1.43.

Steppe, K., Sterck, F., Deslauriers, A., 2015a. Diel growth dynamics in tree stems: linking anatomy and ecophysiology. Trends Plant Sci. 20 (6), 335–343. https://doi.org/10.1016/j.tplants.2015.03.015.

Steppe, K., Vandegehuchte, M.W., Tognetti, R., Mencuccini, M., 2015b. Sap flow as a key trait in the understanding of plant hydraulic functioning. Tree Physiol. 35 (4), 341–345. https://doi.org/10.1093/treephys/tpv033.

Torres-Ruiz, J.M., Cochard, H., Delzon, S., Boivin, T., Burlett, R., Cailleret, M., Corso, D., Delmas, C.E.L., De Caceres, M., Diaz-Espejo, A., Fernández-Conradi, P., Guillemot, J., Lamarque, L.J., Limousin, J.M., Mantova, M., Mencuccini, M., Morin, X., Pimont, F., De Dios, V.R., Ruffault, J., Trueba, S., Martin-StPaul, N.K., 2024. Plant hydraulics at the heart of plant, crops and ecosystem functions in the face of climate change. N. Phytol. 241 (3), 984–999. https://doi.org/10.1111/nph.19463.

Tyree, M.T., Ewers, F.W., 1991. The hydraulic architecture of trees and other woody plants. N. Phytol. 119 (3), 345–360. https://doi.org/10.1111/j.1469-8137.1991.tb00035.x.

Verbeeck, H., Steppe, K., Nadezhdina, N., de Beeck, M.O., Deckmyn, G., Meiresonne, L., Lemeur, R., Čermák, J., Ceulemans, R., Janssens, I.A., 2007. Stored water use and transpiration in Scots pine: a modeling analysis with ANAFORE. Tree Physiol. 27 (12), 1671–1685. https://doi.org/10.1093/treephys/27.12.1671.

Williams, M., Bond, B.J., Ryan, M.G., 2001. Evaluating different soil and plant hydraulic constraints on tree function using a model and sap flow data from ponderosa pine. Plant Cell Environ. 24 (7), 679–690. https://doi.org/10.1046/j.1365-3040.2001.00715.x.

Wu, K., Jia, Z., Duan, Q., 2023. The detection of kiwifruit sunscald using spectral reflectance data combined with machine learning and CNNs. Agronomy 13 (8), 2137. https://doi.org/10.3390/agronomy13082137.

Xiloyannis, C., Dichio, B., Mininni, A.N., 2023. Vine nutrition and water requirement. In: Richardson, A.C., Burdon, J.N., Ferguson, A.R. (Eds.), Kiwifruit: Botany, Production and Uses. CAB International, Boston, pp. 164–183.