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Kiwifruit ecophysiological adaptations under moderate and severe deficit irrigation

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ABSTRACT

Precision irrigation scheduling in fruit crops requires good knowledge of water relations. Knowing plants' behavior and the strategies to be adopted under water stress allows irrigation scheduling to maximize water productivity and minimize water losses. Therefore, the aim of this study is (i) to analyze the relationships between sap flux density, leaf stomatal conductance and fruit diameter daily fluctuations, understanding the water dynamics among plant tissues, and (ii) to understand the effect of deficit irrigation on the fruit size and quality. *Actinidia chinensis* var. *chinensis* vines were submitted to four irrigation treatments, applied as percentages of crop evapotranspiration (ETc): 100 %, 68 %, 57 % and 40 % of ETc. Four vines per treatment were monitored with sap flow probes, using the Tmax method, and the same vines had fruit gauges installed to obtain continuous measurements of fruit diameter variations. Measurements of leaf gas exchange were performed throughout the day on six days during the season. Fruit dry matter content was also measured three times during the season and at harvest, together with fruit quality parameters (soluble solids content, firmness, and titratable acidity) at harvest. The comparison of the daily dynamics of sap flux density and leaf stomatal conductance reveals that sap flow continues rising after the beginning of stomatal closure, indicating refilling of storage tissues such as branches and leaves. However, fruit refilling starts at night, when there is less competition for water. Fruit average diameter ($Ø_f$) was significantly higher at the 68 % ETc treatment in comparison to control (100 % ETc), being this also significantly higher than the other deficit irrigation treatments (57 % and 40 % ETc). A vapor pressure deficit threshold was identified, above which stomata start to close, regardless of irrigation treatment. Deficit irrigation affected negatively kiwifruit vines sap flux density. Optimized irrigation management, avoiding overirrigation, might lead to higher fruit dry matter content without significantly reducing fruit diameter.

1. Introduction

Kiwifruit is widely cultivated in the Mediterranean basin, an environment characterized by high temperatures and solar radiation, with little to no rainfall during summer (Montanaro et al., 2007). These conditions make irrigation a mandatory practice for kiwifruit in this region, as this crop originated in the mountains of South-East China, where rainfall is higher and better distributed during the year (Ferguson, 1984). Therefore, *Actinidia* species did not adapt their leaves, hydraulic characteristics and physiology to drought stress (Torres-Ruiz et al., 2016). Furthermore, kiwifruit vines are characterized as isohydric, which means that this crop has a quick stomatal adjustment, which allows a fast response against water stress, allowing it to maintain higher (less negative) leaf water potential during the day (Boini et al., 2022). However, most kiwifruit irrigation is managed empirically, mainly in regions where the cost of irrigation water is low.

Aiming at improving irrigation decision making, many studies have been performed on the use of plant-based indexes and sensors to improve irrigation water productivity (Fernández, 2017). Besides empirical irrigation management, soil moisture monitoring and meteorological data have been used to schedule irrigation, but these measurements do not provide information on the actual plant water status. Nonetheless, according to Fernández (2017), leaf stomatal conductance (g_s) has a great potential as water stress indicator, being useful for irrigation scheduling. Additionally, the continuous monitoring of fruit diameter variations (Morandi et al., 2007) can provide valuable information on plant water stress and allows the study of water relationships among plant tissues (Boini et al. 2019; Fernandes et al., 2018).

The seasonal growth pattern of the kiwifruit berry is characterized by an initial period of rapid growth, followed by a period of slower growth

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(Miller et al., 1998; Morandi et al., 2010). Morandi et al. (2010) measured vascular flows in kiwifruit throughout the fruit growing season, and observed that berries transpiration decreases with time, being higher initially. These authors also observed that during the initial rapid growth period xylem is the main source of water and nutrients to the fruits, while phloem increases and becomes predominant at the later slower fruit growth period. The higher xylem flows during the initial stages of fruit growth are driven by the high fruit transpiration rates, which on their turn, are due to higher superficial conductance (g_c) (Morandi et al., 2010). According to Clearwater et al. (2012), in the second phase of fruit growth, closer to ripening, the xylem alone is not able to support growth, but balance fruit transpiration. In the second phase of fruit growth, xylem reduced functionality can be attributed to the reduced driving forces responsible for the flow, such as lower fruit transpiration (Clearwater et al., 2012), which is due to lower superficial conductance (g_c) at this phase (Morandi et al., 2010). This is similar to what is observed also in grapevine (Clearwater et al., 2012).

Sap flow measurements can also provide useful information regarding the transpiration and water relations of plants. Sap flow is usually measured indirectly through sap flux density (J_s), which is the amount of sap flowing through a certain surface per time (Vandegehuchte and Steppe, 2013). In other words, the sap flux density is more easily compared between plants of the same treatment, as it does not consider the sap wood area.

Hernandez-Santana et al. (2023) studied the behavior of fruit crops by using well-known indexes already proposed in previous publications, such as the vapor pressure deficit (D) at which maximum J_s occurs (D_{Jsmax}) (Grossiord et al., 2017, 2018), and the sensitivity of J_s to D (m_{Js}) (as proposed by Litvak et al. (2012) based on Oren et al. (1999)). The comparison of these indexes among species can provide useful insights when comparing the effect of deficit irrigation treatments in species adapted to wet climate. For example, species with higher D_{Jsmax} are more tolerant to water deficit. Furthermore, knowing the limitations of the species regarding sap flow is crucial for irrigation decision making.

As far as we know, information is lacking regarding the behavior of sap flux density and leaf gas exchange in kiwifruit under deficit irrigation conditions. Considering this context, this paper aims at (i) analyzing the relationships between sap flux density, leaf stomatal conductance and fruit diameter daily fluctuations to understand the water dynamics among different plant tissues, and (ii) understanding the influence of deficit irrigation on fruit size and quality.

2. Material and methods

2.1. Experimental site and design

The experiment was performed in a commercial orchard in the Po Valley, close to Imola, Italy (coordinates 44° 24′ 37.11″ N, 11° 40′ 42.45″ E), an area characterized by Mediterranean climate, with hot and humid summers and cold, wet winters. The orchard had 8-years-old kiwifruit vines (*Actinidia chinensis* var. *chinensis* cultivar Jintao) distancing 4.5 m between rows and 1.5 m between vines, in a silty clay loam soil (12 % sand, 34 % clay, and 54 % silt). Full bloom occurred on 08 May 2023. The irrigation system consisted of two drip lines located approximately 0.20 m from the vines' trunk and about 0.40 m high. Additionally, there was a line of sprinklers at approximately 0.60 m from the soil and about 0.75 m from the vines. Four irrigation treatments were imposed in six plants (including males) during the whole fruit growing season (from June 7th until harvest) as percentages of crop evapotranspiration (ET_C) reposition through irrigation, being 100, 68, 57 and 40 % of ET_C (henceforth referred as T100, T68, T57, T40, respectively). The experimental design is represented in Fig. S1. The treatments were applied by using drippers of different outflow rates and distances between emitters (i.e., T100: 1.6 L h^{-1} drippers every 0.30 m; T68: 2.0 L h^{-1} drippers every 0.55 m; T57: 2.0 L h^{-1} drippers every 0.65 m; and T40: 1.1 L h^{-1} drippers every 0.50 m). The sprinkler system was used only during the hottest days of summer (ca. mid-august), which can be identified by the high irrigation volumes in Fig. S2. The total amount of irrigation from June 1st until harvest (October 12th) was equal to 415.4, 325.8, 296.3 and 250 mm for the irrigation treatments T100, T68, T57 and T40, respectively, Fig. S2 contains the data regarding irrigation doses, rainfall and ET_C.

2.2. Meteorological conditions

Weather conditions in the kiwifruit orchard were monitored with an external meteorological station placed outside the orchard (ca. 50 m from the orchard). The meteorological station recorded data of rainfall, solar radiation, air relative humidity and temperature. Average values were registered every 15 min and transmitted to the cloud (WiNet s.r.l.). Additionally, air relative humidity and temperature were measured under the shading net (18 % of shading) at 2.5 and 1.5 m from the ground. The measurements from the thermohygrometer at 1.5 m were used to calculate the atmospheric vapor pressure deficit (D, kPa) according to the methodology used to calculate evapotranspiration by FAO 56 (Allen et al., 1998). These parameters were registered on an hourly basis by a dedicated weather station (Davis Instruments GroWeather 24 Hr Fan, Cabled, Metric 6825CM, Davis, CA, USA).

The estimation of crop evapotranspiration (ETc) was performed by the decision support system Irriframe, provided by Canale Emiliano Romagnolo – CER, the agency that regulates the use of water in the Emilia Romagna region. The methodology used by this platform to estimate potential evapotranspiration (ETo) is the one described by Doorembos and Pruitt (1977) in the FAO Irrigation and Drainage paper n. 24. The meteorological variables used to calculate ETo were obtained from a weather station managed by ARPAE, the regional meteorological agency (station 1623 Casola Canina Ovest). The soil water balance is also considered by Irriframe. The crop coefficients used to estimate ETc were also provided by the Irriframe decision support system, being equal to 0.75 during full bloom; 0.85 during fruit set and fruit growth; and 0.75 during fruit maturation until leaves abscission (Allen et al., 1998).

2.3. Physiological measurements

For each irrigation treatment, four female plants were chosen for the sap flow measurements that were carried out using the probes supplied by Tranzflo NZ Ltd. (Palmerston North, New Zealand). The T-max method (Cohen et al., 1981) was chosen to measure sap flux density (J_s, cm h^{-1}) in the kiwi vines, due to its higher adequacy for measuring high sap flow values. The sensing probes had two thermocouples, at 10 and 25 mm, and were positioned at 15 and 40 mm downstream from the heater. A datalogger CR1000 and a multiplexer AM16/32B (Campbell Scientific) were used to activate the heater and monitor the difference in temperature between the sensing probes through single ended connections. The treatments were divided into two sets (each with 8 sap flow sensors, see Fig. S1), the heaters from first set were activated at the minutes 00 and 30 of every hour, for 4 s, with data collection every second for 5 min. The heaters from the second set were activated at the minutes 15 and 45 min of every hour, also for 4 s with data collection every second for 5 min. Eight heat pulse controllers were used to power the heaters and were controlled by the datalogger, being two heaters powered by each heat pulse controller.

To obtain sap flux density (cm h^{-1}) we used the equations reported by Cohen et al. (1981), Green et al. (2003, 2009), as follows:

$$V_M = \sqrt{x_D^2 - 4\kappa t_M / t_M} \quad (1)$$

in which V_M is the heat-pulse velocity (m s^{-1}); x_D is the distance from the heater to the sensor downstream (cm); t_M is the time for maximum difference in temperature between sensors (s); and κ is the thermal diffusivity, which can be determined by applying the following equation:

$$\kappa = x_D^2/4t_M \quad (2)$$

at times when zero sap flow occurs, usually at night. For the experiment described in this manuscript, values of t_M higher than 245 s were assumed to be equal to zero sap flow, which consequently makes κ equal to 0.0023.

These equations assume that the needles (both from heater and thermocouples) have no influence on the measurements. However, there are perturbations that correlated to the wound width. Green et al. (2003) have studied the influence of the wound width and published the correction factors to be used in the following equation:

$$V_C = a_0 + a_1 V_M + a_2 V_M \quad (3)$$

in which V_C is the corrected heat-pulse velocity (m s^{-1}); a_0, a_1 and a_2 are the factors obtained by Green et al. (2003) regarding different wound widths and distances from heater to the closest temperature probe.

Additionally, Green et al. (2003) indicates the need to use an equation to correlate heat-pulse velocity to sap flux density (J_s), as follows:

$$J_s = (kF_M + F_L)V_C \quad (4)$$

where F_M and F_L are the volume fractions of wood and water, respectively. The k factor is related to the thermal properties of the woody matrix (Green et al., 2003). According to calibration experiments performed by Tranzflo NZ Ltd., the k factor for kiwi vines is equal to 0.505 and F_M and F_L are equal to 0.31 and 0.64, respectively.

At nine days during the kiwifruit growing season, mainly during the period of greater water requirement, leaf gas exchange measurements were taken during the day, approximately at every hour. The measurements were taken using the LI-6800 Portable Photosynthesis System (LI-COR®) with the fluorometer chamber, using CO_2 concentration of 400 ppm and no humidity or temperature modifications. The measurements were taken in one leaf per vine, concomitantly to those of sap flow on well-developed, not damaged leaves fully exposed to the sun, using average environmental PAR (photosynthetically active radiation) as input. The average environmental PAR value used for every set of measurements (8 vines) was based on the values provided by the LI-6800 PAR sensor, measured under the shading net, shortly before the sap flow heater was turned on for all the vines in each sap flow set. This approach was used to avoid rapid changes in PAR during the same set of measurements due to cloudy conditions.

For graphical visualization, data regarding sap flux density (J_s) and leaf stomatal conductance (g_s) were averaged by treatment and by time of measurement (g_s was measured every 30 min).

2.4. Fruit growth monitoring

Continuous fruit diameter variations were monitored on 4 fruit per treatment, at short time intervals (15 min), using custom-built fruit gauges interfaced to a wireless data-logger system (WiNet srl, Cesena, Italy). The gauges consist of a light, stainless steel frame supporting a variable linear resistance transducer (Megatron Elektronik AG & Co., Munich, Germany) (Morandi et al., 2007). At installation and during some periodical visits, the actual fruit diameter was measured with a caliper.

Twice during the season eight fruits per treatment were sampled for the determination of the diameter-weight correlation. At harvest, additional eight representative fruits per tree were selected for diameter and weight measurement. The diameter and weight of individual fruits, both during the season and at harvest, were used to obtain a linear regression model ($R^2 \approx 0.9$). This linear model was used to convert fruit diameter into fruit weight, aiming at the calculation of absolute growth rate (AGR) as variation in weight (g 15 min^{-1}).

Fruit seasonal growth was also monitored at regular times intervals during the season using calipers, on 32 fruit per treatment. Fruit diameter variations (mm) monitored with the fruit gauges were converted into fruit mass (g) using the following conversion equation:

$$FW = -147.317 + FDiam_{Max} \cdot 4.914$$

in which FW is the fruit weight, $FDiam_{Max}$ is the kiwifruit maximum horizontal diameter. As yellow fleshed kiwifruits tend to present a flat surface, the maximum diameter was considered.

Unfortunately, in frequent times during the season some fruit gauges did not work properly, for example, fruits might have fallen or slipped from the fruit gauge. Therefore, for graphical representation, when two or more fruit gauges were working well the data is represented as solid lines. On the contrary, dashed lines were used to represent when only one fruit gauge was collecting correct data. The seasonal trend in fruit growth was calculated as the average between the changes in diameter among the working fruit gauges.

2.5. Fruit quality

Twice during the season and at harvest, fruits were collected for the determination of fruit dry matter content. Fruit disks (ca. 1 cm height) from the central region of the fruit were weighted before and after drying at a drying oven at 65 °C until constant weight.

At harvest, 4 fruits per plant were randomly selected (total of 16 fruits per treatment) for the fruit quality analysis of soluble solids content (SSC,°Brix) with a handheld digital refractometer PAL-1 (Atago Italia s.r.l.); firmness (kgf cm^{-2}) with a FTA motorized penetrometer (Turoni s.r.l., Forlì, Italy); titratable acidity (g L^{-1}) with a potentiometric titrator (Tritalab AT1000, Hach) and dry matter content (DM, %) as previously described. Furthermore, all fruits from the four monitored vines were weighed, counted and had their diameter measured, thus obtaining crop load and average diameter ($Ø_f$).

2.6. Data analysis

Data regarding fruit quality was analyzed through Shapiro-Wilk and Breusch-Pagan tests to check for normality and homoscedasticity, respectively. When those precepts were verified, analysis of variance and Tukey HSD post-hoc test were used to check if there were differences between treatments. Otherwise, differences between treatments were checked through Kruskal-Wallis and Wilcoxon post-hoc tests.

The data analysis was performed with R statistical software (R Core Team, 2023) and some of its packages: ggplot2 (Wickham, 2016), ggpubr (Kassambara, 2023), car (Fox and Weisberg, 2019), dplyr (Wickham et al., 2023a) and tidyr (Wickham et al., 2023b).

3. Results

3.1. Sap flux density, leaf stomatal conductance and fruit growth

Daily maximum leaf stomatal conductance ($g_{s.max}$) was limited by water availability during the season, although significant differences were identified only in four days of measurements (Fig. 1). The T100 and T68 presented close values, with some days when $g_{s.max}$ was higher in T68 than in T100 (i.e. 71 and 141 DAFB).

Although leaf gas exchanges were measured in nine days during the fruit growing season, we chose to show only five of these days, selecting the days with days of higher solar radiation. Leaf stomatal conductance (g_s) at 85 DAFB increased from the first measurement (09:00 h) to the fourth measurement (11:30 h) for the T100, T68 and T40 treatments (maximum values 0.313, 0.308 and 0.230 mol m^{-2} s^{-1}, respectively) (Fig. 2A). Subsequently, around 12:00 h, g_s began to decrease more significantly, with minimum values around 15:00 h, being T40 the treatment with lowest values (0.076 mol m^{-2} s^{-1}). Sap flux density (J_s) increased during the day, reaching its maximum value shortly before 15:00 h, followed by a slight decrease (Fig. 2B). Regarding the meteorological conditions, PAR values exceeded 1000 μmol m^{-2} s^{-1} after 11:30

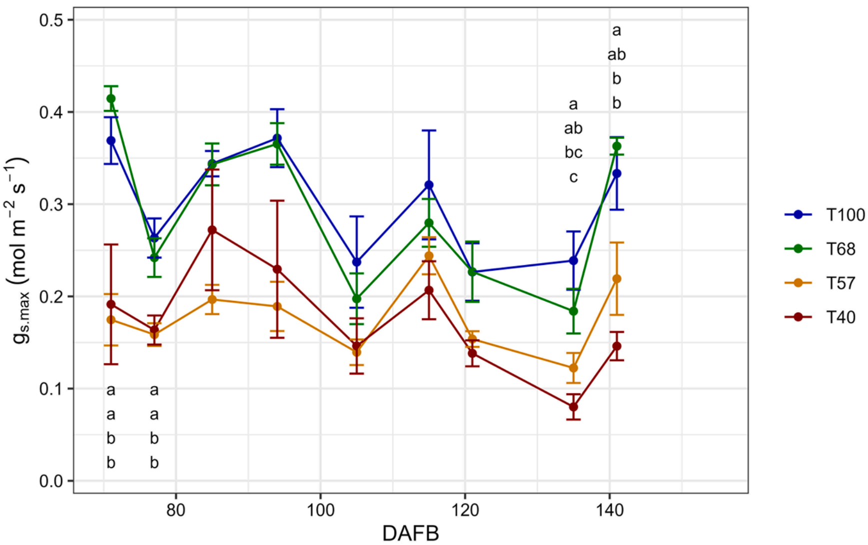

Fig. 1. Seasonal dynamics of daily maximum leaf stomatal conductance ($g_{s,max}$, mol m^{-2} s^{-1}). DAFB – days after full bloom. Different letters identify significant differences between irrigation treatments (p-value < 0.05) according to the Wilcoxon Rank Sum test.

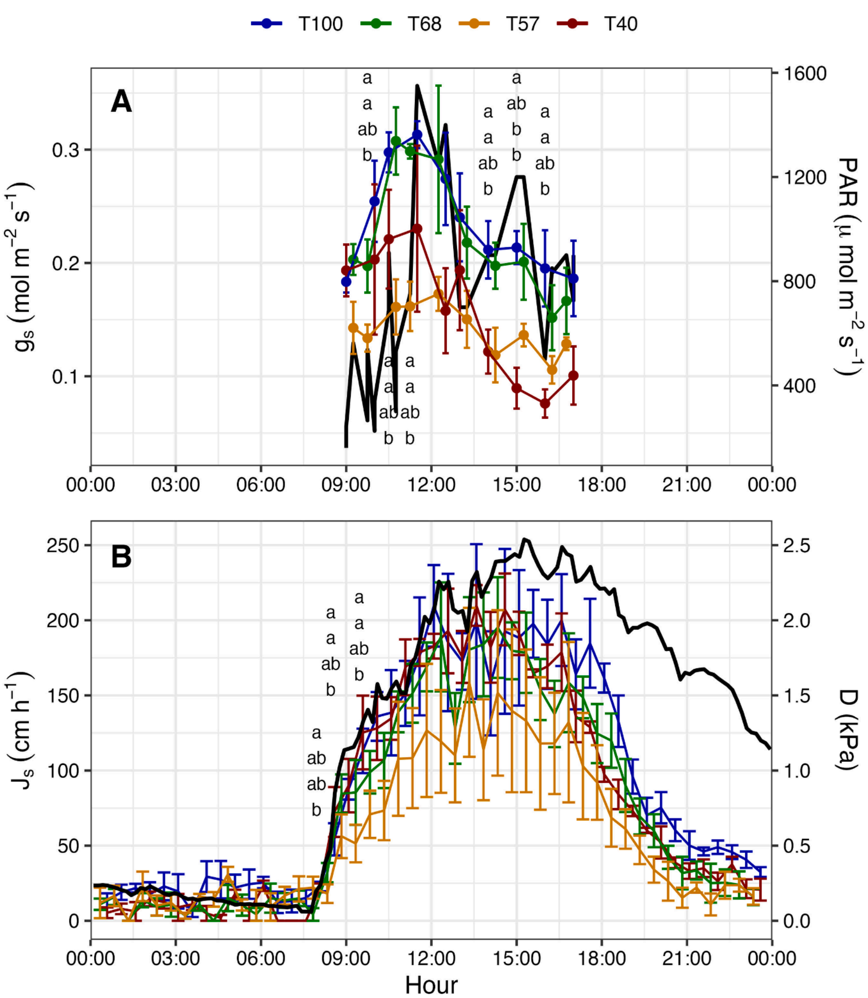

Fig. 2. Diurnal dynamics, at 85 DAFB, of leaf stomatal conductance (±SE) (g_s, mol m^{-2} s^{-1}) and photosynthetic active radiation (PAR, μmol m^{-2} s^{-1}) (A); sap flux density (±SE) (J_s, cm h^{-1}) and vapor pressure deficit (D, kPa) (B). The black lines represent PAR (A) and D (B). Error bars represent standard error (n = 4). Different letters identify significant differences between irrigation treatments (p-value < 0.05) according to the Wilcoxon Rank Sum test.

h, and with increasing D until around 15:00 h, with maximum of approximately 2.5 kPa. Fruit gauges were installed later in the season; therefore, no data is shown for this date.

Leaf stomatal conductance (g_s) at 105 DAFB increased from the first measurement to the second and third measurements for the T100, T68 and T57 treatments (maximum values 0.22, 0.165 and 0.121 mol m^{-2} s^{-1}, respectively) (Fig. 3A). Subsequently, at 11:30 h, g_s begun to decrease more significantly, with minimum values around 15:00 h. Conversely, sap flux density (J_s) increased during the day, reaching its maximum value shortly before 15:00 h, followed by a slight decrease (Fig. 3B). Regarding the meteorological conditions, PAR values exceeded 1000 μmol m^{-2} s^{-1} after 09:00, and with increasing D until around 15:00 h.

Fruit weight started to increase before sunrise for T100 and T40 treatments, until around 12:00 h, followed by a decrease until sunset for the T100, T57 and T40 treatments (Fig. 3D). It is important to consider that the T100 treatment at this day is represented by only one fruit (dashed line).

At 115 DAFB, the g_s daily curve (Fig. 4A) presented an increasing trend from sunrise to noon, for the T100, T68 and T57 treatments, reaching their maximum values (0.304, 0.270 and 0.244 mol m^{-2} s^{-1}, respectively) between 12:00 h and 13:00 h, followed by a slight decrease during the afternoon. The T40 treatment presented a decreasing trend throughout the day. The daily trend of J_s (Fig. 4B) is similar to g_s, but the maximum values were reached slightly later (ca. 13:00 h), except for the T40 treatment which presented maximum J_s around 12:00 h.

Changes in fruit diameter at 115 DAFB (Fig. 4D) presented increasing trends throughout the day, even before sunrise. The T57 and T40 treatments showed steady values after approximately 12:00 h. Considering the meteorological variables, it is evident that the day was mostly shaded, with PAR below 1000 μmol m^{-2} s^{-1} (Fig. 3A) and D below 2 kPa (Fig. 4B).

Leaf stomatal conductance at 121 DAFB (Fig. 5A) presented an initial increasing trend, reaching maximum values around 12:00 h for T100, T68 and T57 (0.195, 0.222 and 0.143 mol m^{-2} s^{-1}, respectively) and around 10:30 h for T40 (0.130 mol m^{-2} s^{-1}), followed by a decreasing trend. On the same day, sap flux density showed an increase until 13:00, except for the T57 treatment, whose stabilization occurred slightly before (around 12:00). All treatments presented a small increase at the last measure (around 15:00 h) (Fig. 5B).

Fruits from the T40 treatment showed diameter increases before sunrise (Fig. 5D) until around 12:00 h, when diameters started to decrease until sunset. Fruits from the other treatments showed a slight decrease just after sunrise, followed by a recovery for the T100 and T68 treatments. The fruits from the T57 treatment, as those from T40 treatment, also presented a decrease in diameter in the afternoon, until sunset. Although being a relatively sunny day, with PAR over 1000 μmol m^{-2} s^{-1}, the vapor pressure deficit exceeded 2.0 kPa only around 15:00 h.

At 141 DAFB, g_s measurements started later (Fig. 6A), the maximum values for T100 and T68 treatments were measured around 10:00 h and 11:30 h, respectively (0.299 and 0.308 mol m^{-2} s^{-1}, respectively), followed by a slight decreasing trend. Leaf stomatal conductance values from the T40 treatment were already low at the beginning of the measurements, with a small increase around 11:00 h, followed by a decrease in the following hours. Regarding the T57 treatment, the maximum g_s value was obtained during the first measurement, followed by a decrease around 11:00 h and a small increase around 11:30 h. On the same day, sap flux density presented an increasing trend, with a stabilization from around 12:00 h for the T68 treatment, while the T100 treatment presented a decrease in J_s at the last measurement. Both T57 and T40 presented a lower and constant increase in J_s values (Fig. 6B).

Regarding changes in fruit diameter at 141 DAFB (Fig. 6D), fruits from all treatments presented decreases of different magnitudes just after sunrise, followed by a great increase in diameter for the T100 and T68 treatments. The T57 treatment, although represented by only one fruit gauge, presented the greatest decrease in diameter until around 12:00 h, when recovery started, overcoming the decrease in diameter suffered during the morning. Yet, for the T40 treatment, although the decrease in diameter in the morning was similar to the T100 treatment,

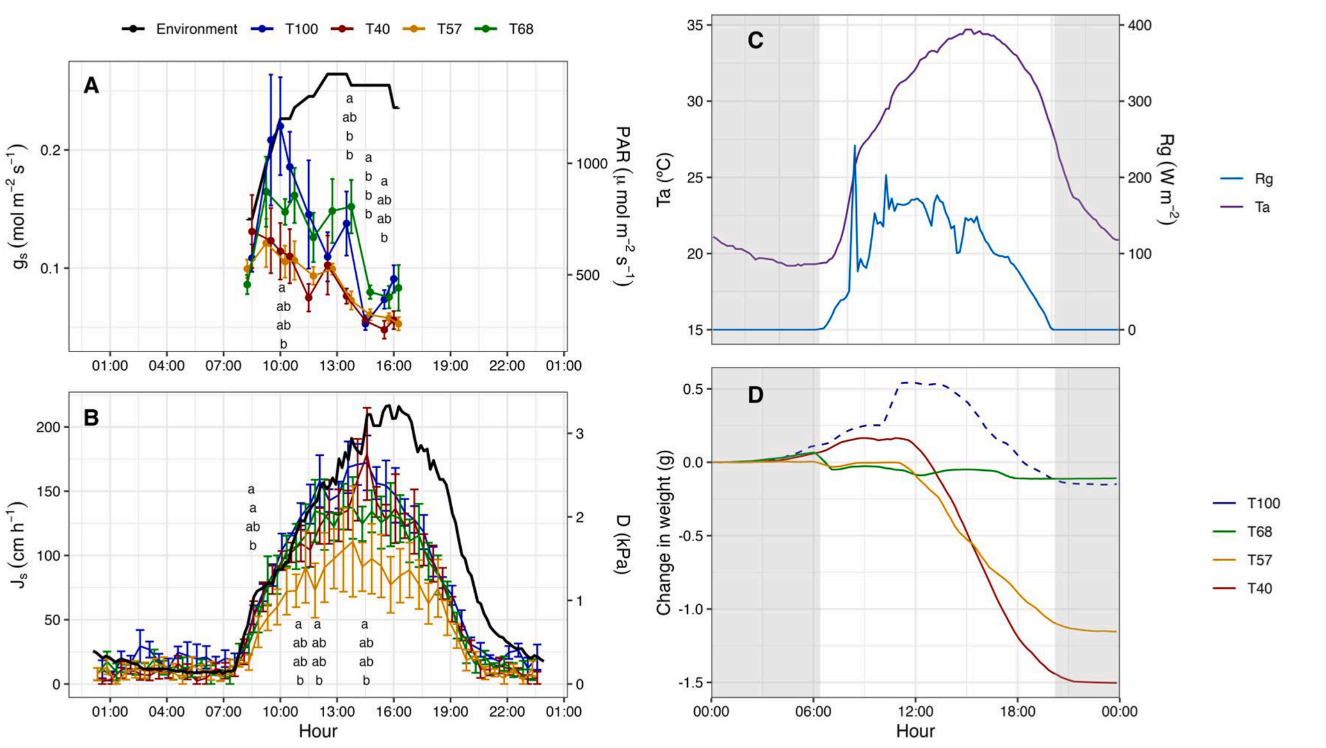

Fig. 3. Diurnal dynamics, at 105 DAFB, of leaf stomatal conductance (±SE) (g_s, mol m^{-2} s^{-1}) and photosynthetic active radiation (PAR, μmol m^{-2} s^{-1}) (A); sap flux density (±SE) (J_s cm h^{-1}) and vapor pressure deficit (D, kPa) (B). Error bars represent standard error ($n = 4$). Air temperature (Ta, °C) and solar radiation (Rg, W m^{-2}) (C); diurnal dynamics of fruit weight (g) (D). Different letters identify significant differences between irrigation treatments (p-value < 0.05) according to the Wilcoxon Rank Sum test.

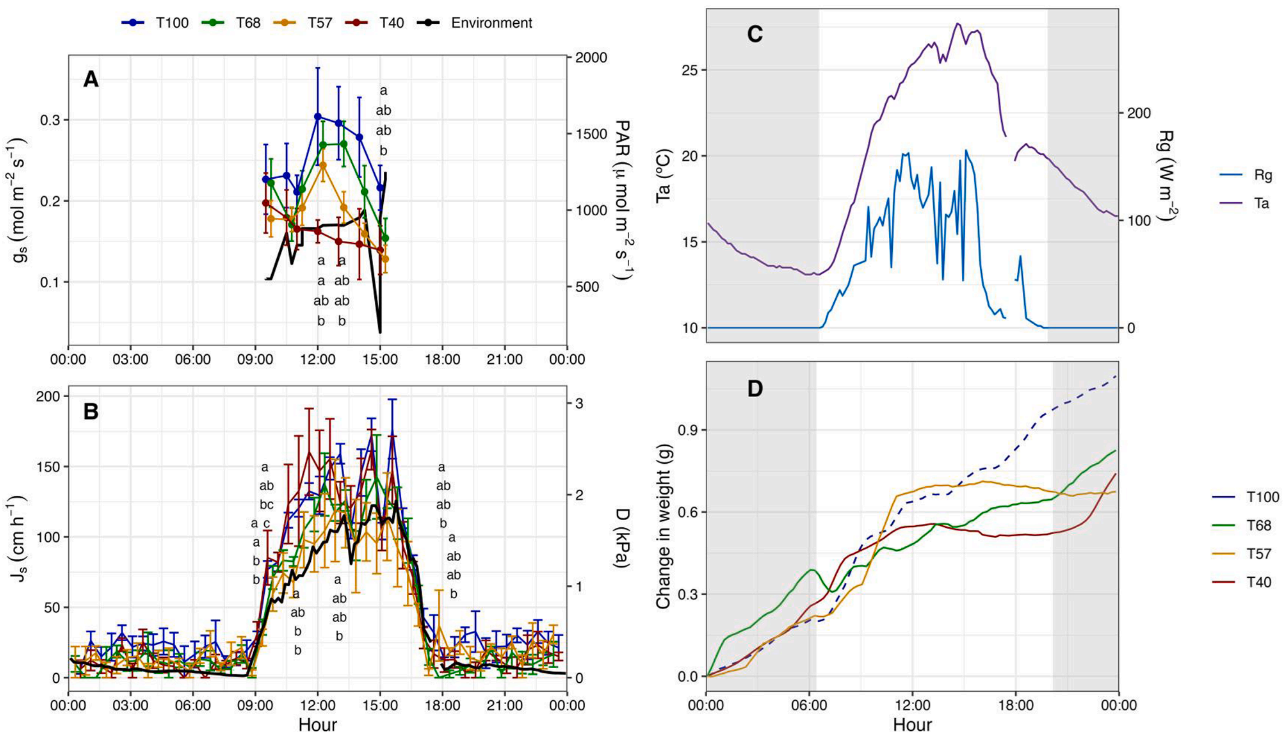

Fig. 4. Diurnal dynamics, at 115 DAFB, of leaf stomatal conductance (±SE) (g_s, mol m^{-2} s^{-1}) and photosynthetic active radiation (PAR, µmol m^{-2} s^{-1}) (A); sap flux density (±SE) (J_s, cm h^{-1}) and vapor pressure deficit (D, kPa) (B). Error bars represent standard error ($n = 4$). Air temperature (Ta, °C) and solar radiation (Rg, W m^{-2}) (C); diurnal dynamics of fruit weight (g) (D). Different letters identify significant differences between irrigation treatments (p-value < 0.05) according to the Wilcoxon Rank Sum test.

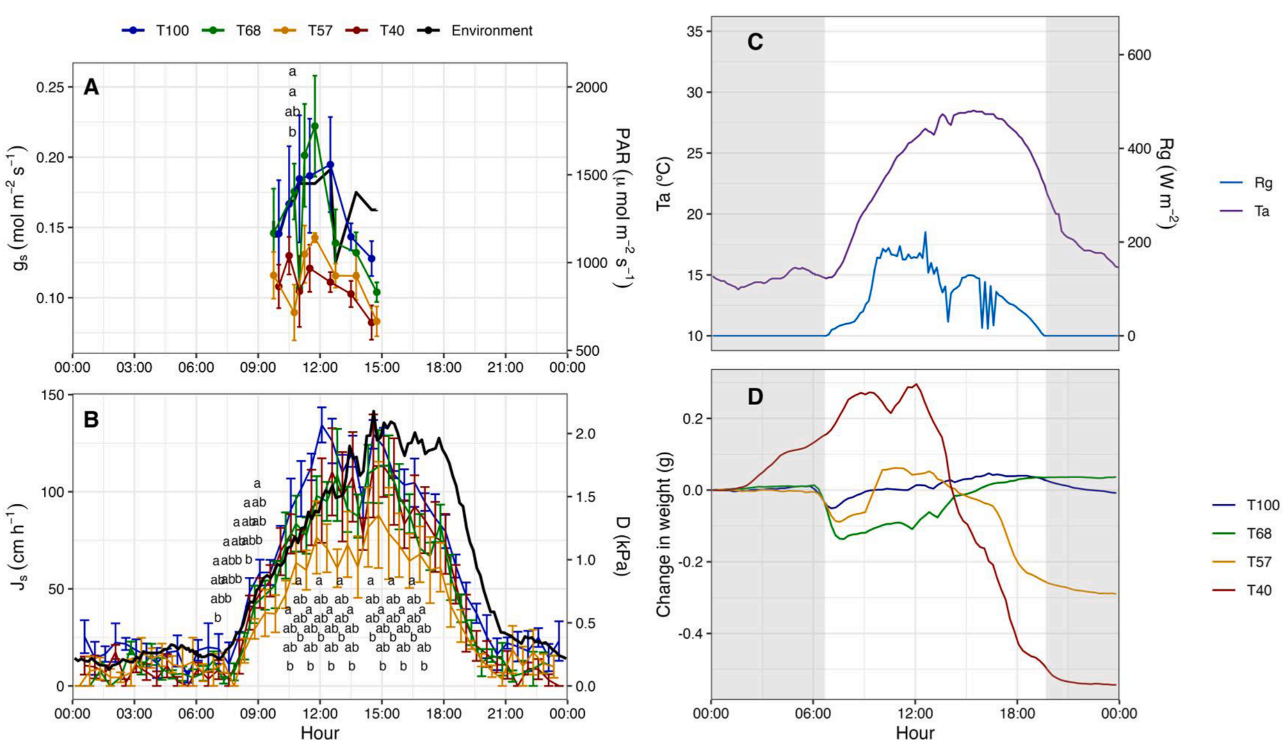

Fig. 5. Diurnal dynamics, at 121 DAFB, of leaf stomatal conductance (±SE) (g_s, mol m^{-2} s^{-1}) and photosynthetic active radiation (PAR, µmol m^{-2} s^{-1}) (A); sap flux density (±SE) (J_s, cm h^{-1}) and vapor pressure deficit (D, kPa) (B). Error bars represent standard error ($n = 4$). Air temperature (Ta, °C) and solar radiation (Rg, W m^{-2}) (C); diurnal dynamics of fruit weight (g) (D). Different letters identify significant differences between irrigation treatments (p-value < 0.05) according to the Wilcoxon Rank Sum test.

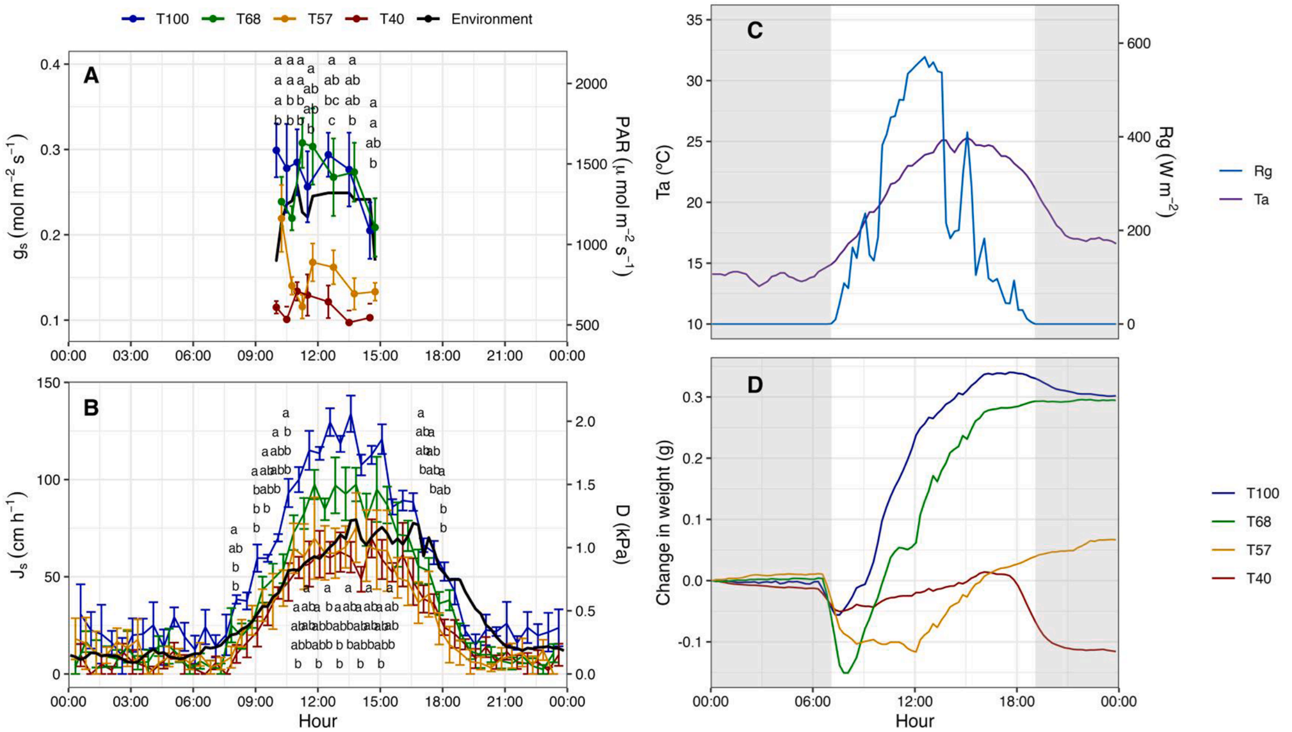

Fig. 6. Diurnal dynamics, at 141 DAFB, of leaf stomatal conductance (±SE) (g_s, mol m^{-2} s^{-1}) and photosynthetic active radiation (PAR, μmol m^{-2} s^{-1}) (A); sap flux density (±SE) (J_s, cm h^{-1}) and vapor pressure deficit (D, kPa) (B). Error bars represent standard error ($n = 4$). Air temperature (Ta, °C) and solar radiation (Rg, W m^{-2}) (C); diurnal dynamics of fruit weight (g) (E). Different letters identify significant differences between irrigation treatments (p-value < 0.05) according to the Wilcoxon Rank Sum test.

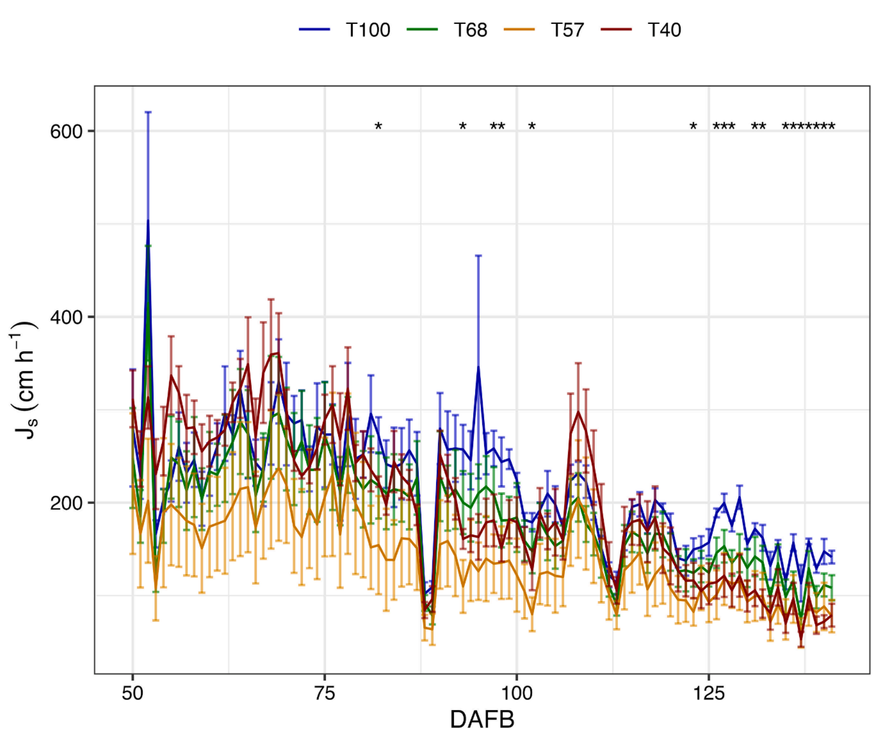

Fig. 7. Seasonal variation of maximum sap flux density (J_s, cm h^{-1}). Error bars represent the standard error of the mean ($n = 4$). Asterisks represent days at which maximum J_s among irrigation treatments was significantly different (p-value < 0.05) according to the Wilcoxon Rank Sum test.

it presented a small recovery until shortly before 18:00 h, when another decrease in diameter occurred until sunset. Although being a sunny day, with PAR over 1250 μmol m^{-2} s^{-1} for most part of the day, the vapor pressure deficit did not exceed 1.2 kPa throughout the day.

Daily maximum sap flux density (J_s) behavior throughout the season was similar among the treatments (Fig. 7), with higher values at the beginning, followed a decreasing trend, mainly after 100 DAFB, which agrees with the decreasing trend presented by crop evapotranspiration

(ETc, Fig. S2). The period when most of the significant differences among irrigation treatments were identified regarding J_s was at the end of the fruit growing season (after DAFB 120), corresponding to the period with lower rainfall. The seasonal maximum J_s average by treatment was 503.46, 414.53, 237.45, and 360.94 for the irrigation treatments T100, T68, T57 and T40, respectively. The seasonal maximum were obtained at 52 DAFB for the T100 and T68 irrigation treatments and at 69 DAFB for the T57 and T40 treatments.

Changes in fruit diameter during the season were also influenced by water availability among the irrigation treatments (Fig. 8). Similarly to the seasonal dynamics of maximum daily leaf gas exchange (Fig. 1), the T100 and T68 treatments presented very similar trends regarding fruit growth. The soil water available to the vines submitted to the treatments T57 and T40 was a limiting factor. These treatments were more influenced by the sprinkler irrigation at 103, 106 and 107 DAFB (Fig. S1).

Aiming at providing insights regarding the limitation of stomatal conductance when atmospheric vapor pressure deficit is above a certain value, the values of g_s, PAR and D were plotted (Fig. 9), including all irrigation treatments. The blue line represents a local polynomial fit ("loess") obtained with the maximum g_s values for each range of 0.1 kPa of D. The g_s values increase with the increase of D, reaching a plateau at D between 1 and 2 kPa (approximately). Regarding the relation between PAR and g_s, it is possible to observe PAR values close to 1500 μmol m^{-2} s^{-1} throughout the range of D.

3.2. Fruit quality

Fruit quality data showed significant differences among the irrigation treatments for most of the analyzed indexes (Table 1). All irrigation treatments differed significantly from each other in terms of fruit average diameter ($Ø_f$), with T68 showing the highest average.

Fruit firmness and acidity were significantly lower for the T100 treatment in comparison to the deficit irrigated treatments (i.e. T68, T57 and T40). In contrast, fruits from the T100 treatment presented significantly lower dry matter contents (DM) when compared to the T57 and T40 treatments. The T57 treatment resulted in higher DM (19.97 %), being significantly higher than T68 and T100 (18.55 % and 18.32 %, respectively), and T40 fruits DM (19.28 %) were not significantly different from T57.

In terms of fruit soluble solid content (SSC), the highest water deficit treatment (T40) showed the highest value (12.86°Brix), being significantly higher than the values obtained for T100 and T68 (10.97 and 10.68°Brix).

No significant differences among treatments were identified regarding yield, and crop load (F_{load}, fruits $plant^{-1}$) (Table 2). Only average fruit weight showed significant differences among treatments, being T68 significantly higher than the higher water deficit treatments (T57 and T40). Although not significantly different, average fruit weight for T68 (112.49 g $fruit^{-1}$) was also higher than the value obtained by the T100 treatment (84.87 g $fruit^{-1}$).

4. Discussion

4.1. Environmental effects on g_s and J_s

The daily patterns of stomatal conductance and the continuous measurement of sap flux density and fruit diameter variations provide useful information to understand the water relationships between fruits, leaves and the water uptake by the kiwi vines.

The influence of vapor pressure deficit (D, kPa) on kiwi vines sap flux density (J_s) and leaf stomatal conductance (g_s) is evident. In Fig. 3, it is noticeable that the stomatal closure happened much earlier (around 12:00 h) than the stabilization of J_s at its maximum value (around 14:00 h), which indicates that water uptake after 12:00 h occurred most probably to refill storage tissues.

In contrast, Figs. 4 and 6 show data collected during days with lower D. In these conditions, the time when maximum g_s and maximum J_s occurred for the T100 and T68 treatments was closer (around 11:00 h and 12:00 h, respectively) in comparison with the data from Fig. 2.

Observing the data on g_s and J_s, we can notice that there are threshold D values for maximum g_s and for J_s under well-watered conditions or minor water deficit. In particular, data from Figs. 2 and 4 suggests that kiwifruit vines have a threshold of about 1.8 to 2 kPa above which stomata start to close, regardless of the water availability. The data from Figs. 2 and 4 sustain that under 2 kPa well irrigated kiwifruit vines are able to keep stomata aperture. This is an important information, as the knowledge on whether the plant can continue to extract water from the soil at days with high D can provide valuable inputs for the irrigation management as well as indications regarding the possibility to reduce VPD, as in the study by Calderón-Orellana et al. (2021), who applied plastic cover in kiwifruit orchards, reducing D at late season. Similarly, Hernandez-Santana et al. (2023) found threshold D values for maximum J_s for five fruit crops in well-watered conditions, being lemon the species with lowest D at which J_s is maximum (c.a. 3

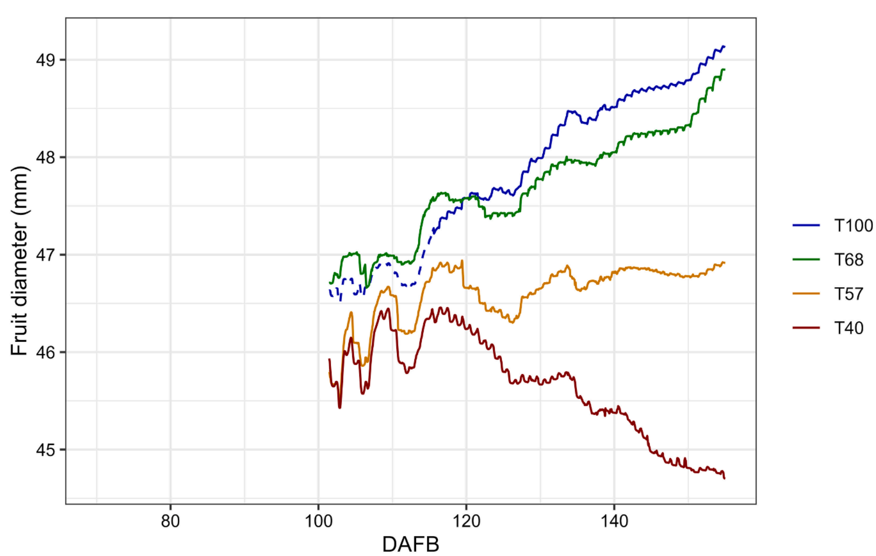

Fig. 8. Seasonal dynamics of fruit diameter (mm) measured by fruit gauges. DAFB – days after full bloom. Dashed line represents a period in which there was only one fruit gauge collecting data in the treatment T100.

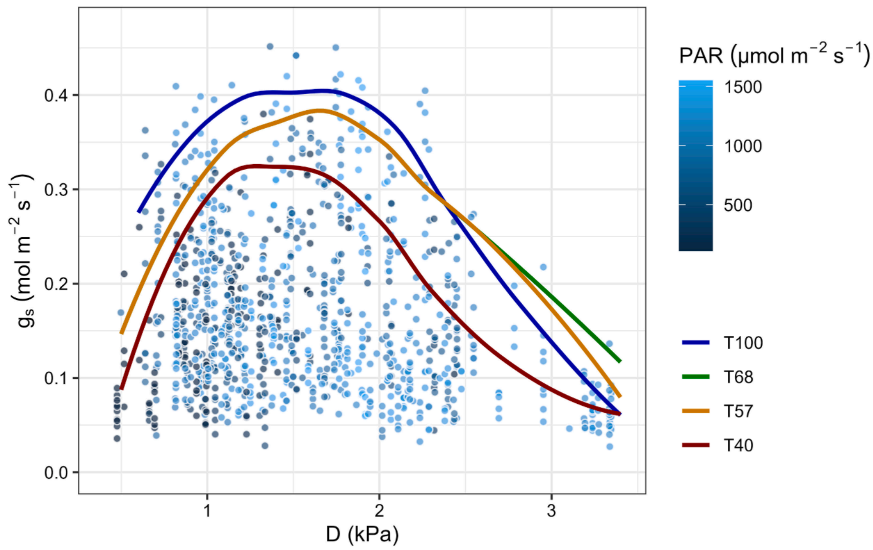

Fig. 9. Relation between leaf stomatal conductance (g_s, mol m^{-2} s^{-1}), atmospheric vapor pressure deficit (D, kPa) and photosynthetically active radiation (PAR, µmol m^{-2} s^{-1}). The colored lines represent the local polynomial regression fit obtained from the maximum values of g_s for each range of 0.1 kPa of D.

Table 1
Fruit quality data (average ± standard error) regarding fruit diameter (Ø$_f$, cm), firmness (kgf cm^{-2}), soluble solid content (SSC,°Brix), dry matter content (DM, %) and titratable acidity (g L^{-1}). Different letters represent significant difference between treatments (p-value < 0.05, according to Tukey test for SSC, Firmness, DM, acidity; and according to Wilcoxon test for Ø$_f$).

Treatment	Ø$_f$	Firmness	SSC	DM	Acidity
T100	47.69 ± 0.239 b	4.74 ± 0.183 b	10.97 ± 0.065 bc	18.32 ± 0.195 c	11.81 ± 0.645 b
T68	48.66 ± 0.246 a	5.44 ± 0.125 a	10.68 ± 0.061 c	18.55 ± 0.295 bc	14.42 ± 0.725 a
T57	45.40 ± 0.241 c	5.60 ± 0.109 a	12.14 ± 0.080 ab	19.97 ± 0.404 a	14.92 ± 0.311 a
T40	43.06 ± 0.271 d	5.56 ± 0.207 a	12.86 ± 0.077 a	19.28 ± 0.413 ab	14.70 ± 0.566 a

Table 2
Kiwifruit productivity data (average ± standard error): fruit yield (kg plant^{-1}), weight per fruit (W$_f$, g fruit^{-1}) and crop load (F$_{load}$, fruits plant^{-1}). Different letters represent significant difference between treatments (p-value < 0.05, according to the Wilcoxon test).

Treatment	Yield	W$_f$	F$_{load}$
T100	7.810 ± 1.464	84.87 ± 1.898 ab	91.50 ± 15.80
T68	7.935 ± 1.079	112.49 ± 21.55 a	74.00 ± 11.26
T57	6.085 ± 1.580	77.32 ± 4.405 bc	80.75 ± 22.09
T40	5.125 ± 1.303	63.32 ± 5.289 c	78.25 ± 13.56

kPa). However, in a recent study Calabritto et al. (2024) reported that kiwifruit vines in the south of Italy did not present limitations of g_s regarding high D. These authors reported D values up to 4 kPa, similar to the present study, but with no reduction of g_s for D over 2 kPa. A possible explanation for the different results obtained in the present study and the study by Calabritto et al. (2024) is the difference in soil texture, as the experiment reported by these authors was performed in a soil with higher percentage of sand. Soils with a higher percentage of sand present higher hydraulic conductivity and, therefore, higher soil-plant hydraulic conductivity ($k_{S\text{-}P}$). The study by Saliendra et al. (1995) on *Betula occidentalis* and the influence of $k_{S\text{-}P}$ on the leaf stomatal conductance (g_s) showed a linear correlation between these variables. Another possible explanation for the difference between the results obtained in the present study and those reported by Calabritto et al. (2024) is that the experiments were performed with different cultivars, which might present different responses to high D.

The local polynomial regression curves represented in Fig. 9 regarding each treatment are slightly different regarding the value of D at which the g_s starts to fall. Despite these small differences among treatments, it is possible to infer that at D above 2.0 kPa (approximately), stomata closure occurs. However, an alternative hypothesis is that a day with high evaporative demand could cause a localized water deficit close to the root zone (Hutton and Loveys, 2011). In a day with high D, the plant would transpire more and absorb the water easily available, reducing its availability in the vadose zone, reaching a threshold value of soil water content below which stomata closure occurs. This is a possible explanation considering the fine texture of the soil in which the present study was performed.

Despite the alternative hypothesis to explain the decrease in g_s above a certain value of D, the fact that all irrigation treatments presented the same behavior (Fig. 9), makes it less probable. In other words, if T57 and T40 also presented a reduction in g_s when D was high, it probably means that the soil water availability was not the most influencing factor. These results agree with those reported by Torres-Ruiz et al. (2016), who compared morning and afternoon irrigation in kiwifruit vines. These authors reported a decrease in g_s even when irrigation was applied in the afternoon hours, moment of highest D during the day.

Considering that the irrigation was split into two applications (one in the morning hours and one in the early afternoon) on many of the days when the leaf gas exchange measurements were performed (Fig. S3), it is possible to assume that the kiwifruit vines from T100 treatment had water available in the soil during the afternoon.

Furthermore, the lack of correlation between g_s and PAR (Fig. 9) agrees with the results reported by Mills et al. (2009), who reported light curves (g_s vs PAR) of potted plants exposed to full-irrigation and reduced irrigation. These authors reported an almost horizontal response of g_s to PAR.

4.2. *Irrigation effect on g_s and J_s*

Besides the influence of vapor pressure deficit (D) on g_s, deficit irrigation treatments also affected leaf stomatal conductance throughout the day and throughout the season, by reducing g_s maximum values, even in those days with lower vapor pressure deficit (Figs. 4 and 6). The highest water deficit treatments (T57 and T40) presented the highest g_s difference from T100. These treatments imposed limiting conditions for the vines, regarding soil water content, negatively affecting the daily maximum leaf stomatal conductance (Fig. 1). These results agree with those obtained by Montanaro et al. (2007). These authors reported g_s measurements in field grown kiwifruit vines under full-irrigation and deficit irrigation, being g_s lower in deficit irrigated vines.

The treatment with 68 % ETc presented very similar results to those obtained from T100. In terms of J_s, the greater differences regarding the irrigation treatments occurred at 141 DAFB. On the other days, the T57 treatment presented lower J_s values, probably due to the placement of the probes in a less conductive part of the trunk of some vines. This could also explain the higher values of standard error of this treatment.

Unfortunately, there is not much literature on the effect of deficit irrigation treatments on sap flow or leaf stomatal conductance in kiwifruit vines. To our knowledge, the only publication regarding kiwifruit g_s responses to deficit irrigation is the study performed by Boini et al. (2022). These authors reported a deficit irrigation treatment (70 % sustained deficit irrigation) in contrast to a full irrigated treatment. Physiological measurements were performed at 09:00, 12:30 and 15:30 h from June to September on *Actinidia chinensis*. Significant differences in g_s were first noticed by these authors at 12:30 h in June, later in July and August in every measurement. While full irrigated vines presented values of g_s up to 0.63 mol m^{-2} s^{-1}, deficit irrigated vines reached a maximum g_s of 0.37 mol m^{-2} s^{-1}. Several researchers used leaf stomatal conductance to assess fruit crops water status (e.g. Boini et al., 2019; Fernandes et al., 2018, 2021; Mills et al., 2009; Montanaro et al., 2007; Padilla-Díaz et al., 2016, 2018; Torres-Ruiz et al., 2016). The daily maximum value of leaf stomatal conductance ($g_{s,max}$) is widely used as a water stress indicator (Fernández, 2017). Therefore, g_s is considered in this publication as a valid measurement to assess the effect of the irrigation treatments applied.

Regarding J_s, there are some studies in literature regarding the response of kiwifruit vines sap flow to the time of irrigation application (Torres-Ruiz, et al. 2016), to partial root zone irrigation after a drought period (Green and Clothier, 1995), and to root pruning (Black et al., 2011), but none of them studied how reduced irrigation affects sap flow. Therefore, to our knowledge, the present study is the first one to report the influence of deficit irrigation on the sap flow. Sap flux density of kiwifruit vines exposed to deficit irrigation was not significantly different from the J_s of well-watered vines at the beginning of the irrigation season (i.e. before 80 DAFB, Fig. 6), when there were some rainfall events (Fig. S2). Later in the season, the deficit irrigation treatments presented significant differences in comparison to T100. For example, at 93 DAFB, average J_s for the T100 treatment (257.18 cm h^{-1}) was significantly higher than for the T57 and T40 treatments (160.95 and 109.90 cm h^{-1}). Closer to harvest (after 130 DAFB), there were some days when only J_s from T40 was significantly lower than J_s from the T100 treatment, as in 128 DAFB, when the averages were 174.90 and 105.84 cm h-1 for the T100 and T40 treatments, respectively.

Green and Clothier (1995) reported maximum J_s values of up to 1 mm s^{-1} in well-watered vines, which is equivalent to 360 cm h^{-1}, being similar to the peak values reported in the present study at the beginning of the irrigation season (before 80 DAFB), which might be due to the differences regarding meteorological conditions to which the vines were submitted in each study.

4.3. Consequences on fruit growth

Decreases in fruit size occurred in the afternoon of days with high D (i.e. 105 DAFB Fig. 3 and 121 DAFB Fig. 5), mainly on water deficit treatments. A possible explanation for this fact is that, although fruit transpiration is reduced in the second phase of growth (Morandi et al., 2010), the xylem hydraulic resistance increases at the same time (Clearwater et al., 2012). Clearwater et al. (2012) argue that at higher D, both fruit and shoot transpiration raise, causing a faster decrease in shoot xylem pressure in contrast with xylem pressure at the fruit side of the pedicel. With this, a decrease occurs in the pressure gradient of the pedicel, causing a reduction of sap flow. These authors compare the fruit to shoot hydraulic system to an electric system, being the fruit compared to a capacitor that can discharge or recharge across a resistor (the shoot hydraulic resistance). According to these authors, with the decrease in pressure gradient across the pedicel, the sap flow into the fruit remains reduced until the fruit, as a capacitor, has discharged into the pedicel through backflow, and the pressure gradient is restored. Therefore, at days of high D, as vascular flows into the fruit are reduced, fruit transpiration overcomes xylem inputs. Therefore, as Clearwater et al. (2012) did, we hypothesize that at higher D, beyond losses from fruit transpiration, fruits might also work as water storage tissue (capacitor), providing water for the pedicel and shoot.

At days of lower D (115 DAFB Fig. 4 and 141 DAFB Fig. 6), fruit relative growth presented a stabilization in the afternoon, sometimes with a much smaller decrease. In these cases, our hypothesis is that as D was not limiting for J_s nor for g_s, the shoot-to-fruit water potential gradient is not enough to cause significant decreases in fruit relative growth. This hypothesis agrees with the findings by Torres-Ruiz et al. (2016), who performed an experiment regarding time of irrigation in kiwifruit orchards. These authors reported steady fruit growth in the afternoon of days with low D, being inflow greater than fruit transpiration, which did not occur in days with higher D. Although fruit water potential was not measured in this study, our hypothesis is based on knowledge from the literature regarding water potential gradient and hydraulic aspects of kiwi vines (e.g. Torres-Ruiz et al., 2016; Boini et al., 2022).

4.4. Effects of different fruit growth on fruit quality as a response to irrigation

Considering that this study reports the data concerning one-year of experiment, it is not possible to consider the results regarding fruit yield and fruit load as significant. Further research is required, with at least two years of experiments, to provide relevant information regarding yield, fruit load and water productivity. However, the present study indicates, from the physiological performance (Figs. 1 and 7) and fruit growth (Fig. 8), that sustained deficit irrigation with percentages equal to or lower than 57 % of ETc are not adequate for yellow fleshed kiwifruit orchards.

Even though no significant difference was observed in terms of yield or fruit load (Table 2), this data provides valuable information on the influence of the irrigation treatments in the fruit growth. Although presenting the lowest fruit load, T68 presented the highest values regarding yield and weight per fruit, as mentioned before.

Fruit relative growth was also affected by the irrigation treatments, with more negative values for T57 and T40 at days with high vapor pressure deficit, but also with higher recovery growth when D was lower (121 DAFB). Fruit growth under water limited conditions is negatively affected by the lack of cell turgor, which is required for fruit growth (Lalonde et al., 2003; Morandi et al., 2010; Patrick, 1990, 1997).

In general, the results presented in this study regarding fruit size, weight, and quality aspects at harvest, agree with those obtained by Zheng et al. (2023). These authors also obtained significant differences between control and deficit irrigation treatments, where the less severe deficit irrigation treatments (i.e. 75 and 85 % ET_C) presented higher fruit volume, higher fruit weight, lower firmness, lower dry matter content, lower soluble solids content and lower titratable acidity in comparison to the control treatments, although the differences were not significant. The results presented in this study regarding dry matter content are also in agreement with those reported by Zheng, where the 55 % ETc treatment presented the highest dry matter content.

Dry matter content (DM) is of great interest for kiwifruit farmers, as some companies pay growers also based on this parameter. In fact, kiwifruit harvest decision making is also based on fruit dry matter content as it might be considered as an indicator of the total fruit carbohydrate, including starch that will be converted into soluble sugars during fruit ripening (Burdon et al., 2004). In the present study it is noticeable that the T57 deficit irrigation treatment (57 % ETc) can improve kiwifruit DM values, although presenting a significant reduction in fruit size. Therefore, we hypothesize that a regulated deficit irrigation strategy could improve DM without great losses in fruit weight. It is well known that kiwifruit final size is defined during the first fast growing phase, while most of the berry dry matter accumulation occurs during the second phase of slower growth. Our hypothesis is that a light deficit or full irrigation during the first phase, followed by a moderate deficit irrigation during the second phase could mostly benefit fruit growth and dry matter accumulation. A similar approach has been achieved in olives (Fernández et al., 2013). Although presenting a different growth pattern and stomatal control behavior, there is a phase of higher irrigation requirement, during which the final fruit size is defined, followed by a phase in which water deficit does not impact greatly on final fruit size.

It is not clear whether the higher values regarding soluble solids content or the higher values of titratable acidity in the deficit irrigation treatments are related to osmotic adjustment in the fruits. Some authors argue that higher SSC values in fruits from deficit irrigated orchards might be explained to the osmotic adjustment, which is a strategy adopted by many plants to maintain turgor in the cells (Barry et al., 2004; Huang et al., 2000; Romero et al., 2006). Other authors argue that high SSC values are measured in fruits from the deficit irrigated vines due to fruit dehydration (Gonzalez-Altozano and Castel, 1999). Considering the data presented, the treatment with highest and lowest SSC was T40 and T100, respectively. Comparing the values of dry matter (DM) between these treatments, we obtain a difference of approximately 4.98 %, which is much lower than the difference in terms of SSC, about 14.70 %. Therefore, we hypothesize that the accumulation of SSC in the more stressed treatments is mainly due to osmotic adjustment, but we cannot exclude the possibility of concentration due to dehydration.

5. Conclusions

Based on the results obtained in the present study, we can conclude that a threshold of vapor pressure deficit (D) was found, above which stomata closure occurs, which is approximately between 1.8 and 2 kPa. It is worth mentioning that the reduction in stomatal conductance when D was above this threshold was seen regardless of the irrigation treatment.

The results also led us to the conclusion that sap flux density can be limited when kiwifruit vines are submitted to stress due to water shortage. In well-watered treatment, when D is above the threshold mentioned above, sap flux density continues, even when stomata start to close, most probably to refill storage tissues.

Data regarding fruit dry matter content and size provide relevant inputs for the correct irrigation management of kiwifruit orchards. It is possible to affirm that optimizing irrigation management, avoiding overirrigation, might lead to higher fruit dry matter content without significantly reducing fruit size.

Further research is required to improve the knowledge of the impact of sustained and regulated deficit irrigation on kiwifruit vines. Regulated deficit irrigation, reducing the irrigation volumes during the second phase of slower fruit growth, could promote higher dry matter content.

CRediT authorship contribution statement

Rafael Dreux Miranda Fernandes: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Melissa Venturi:** Writing – review & editing, Project administration, Methodology. **Andrea Giovannini:** Writing – review & editing, Visualization, Methodology, Investigation. **Brunella Morandi:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Rafael Dreux Miranda Fernandes reports financial support was provided by Horizon Europe. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.scienta.2025.114193.

Data availability

The data will be made available through Zenodo repository.

References

Allen, R., Pereira, L.S., Raes, D., Smith, M., 1998. Crop Evapotranspiration - Guidelines for Computing Crop Water Requirements. FAO Irrigation and Drainage, Rome.

Barry, G.H., Castle, W.S., Davies, F.S., 2004. Rootstocks and plant water relations affect sugar accumulation of citrus fruit via osmotic adjustment. J. Am. Soc. Hortic. Sci. 129, 881–889. https://doi.org/10.21273/jashs.129.6.0881.

Boini, A., Manfrini, L., Bortolotti, G., Corelli-Grappadelli, L., Morandi, B., 2019. Monitoring fruit daily growth indicates the onset of mild drought stress in apple. Sci. Hortic. 256, 108520. https://doi.org/10.1016/j.scienta.2019.05.047.

Black, M.Z., Patterson, K.J., Minchin, P.E.H., Gould, K.S., Clearwater, M.J., 2011. Hydraulic responses of whole vines and individual roots of kiwifruit (Actinidia chinensis) following root severance. Tree Physiol. 31 (5), 508–518. https://doi.org/10.1093/treephys/tpr045.

Boini, A., Cavallina, L., Perulli, G., Bresilla, K., Bortolotti, G., Morandi, B., Corelli Grappadelli, L., Manfrini, L., 2022. Actinidia chinensis: physiological and productive performance under water stress condition. Acta Hortic. 1346, 43–50. https://doi.org/10.17660/ActaHortic.2022.1346.6.

Burdon, J., McLeod, D., Lallu, N., Gamble, J., Petley, M., Gunson, A., 2004. Consumer evaluation of "Hayward" kiwifruit of different at-harvest dry matter content. Postharvest Biol. Technol. 34 (3), 245–255. https://doi.org/10.1016/j.postharvbio.2004.04.009.

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.

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.

Clearwater, M.J., Luo, Z., Ong, S.E.C., Blattmann, P., Thorp, T.G., 2012. Vascular functioning and the water balance of ripening kiwifruit (*Actinidia chinensis*) berries. J. Exp. Bot. 63 (5), 1835–1847. https://doi.org/10.1093/jxb/err352.

Cohen, Y., Fuchs, M., Green, G.C., 1981. Improvement of the heat pulse method for determining sap flow in trees. Plant Cell Environ. 4, 391–397. https://doi.org/10.1111/j.1365-3040.1981.tb02117.x.

Doorembos, J., Pruitt, W.O. 1977. Guidelines for predicting crop water requirement. FAO Irrigation and Drainage Paper n.24.

Ferguson, A., 1984. Kiwifruit: a botanical review. 10.1002/9781118060797.ch1.

Fernandes, R.D.M., Cuevas, M.V., Diaz-Espejo, A., Hernandez-Santana, V., 2018. Effects of water stress on fruit growth and water relations between fruits and leaves in a hedgerow olive orchard. Agric. Water. Manage 210, 32–40. https://doi.org/10.1016/j.agwat.2018.07.028.

Fernandes, R.D.M., Egea, G., Hernandez-Santana, V., Diaz-Espejo, A., Fernández, J.E., Perez-Martin, A., Cuevas, M.V., 2021. Response of vegetative and fruit growth to the soil volume wetted by irrigation in a super-high-density olive orchard. Agric. Water. Manage 258, 107197. https://doi.org/10.1016/j.agwat.2021.107197.

Fernández, J.E., Perez-Martin, A., Torres-Ruiz, J.M., et al., 2013. A regulated deficit irrigation strategy for hedgerow olive orchards with high plant density. Plant Soil. 372, 279–295. https://doi.org/10.1007/s11104-013-1704-2.

Fernández, J.E., 2017. Plant-based methods for irrigation scheduling of woody crops. Horticulturae 3, 35. https://doi.org/10.3390/horticulturae3020035.

Fox, J., Weisberg, S., 2019. An R Companion to Applied Regression, 3rd ed. Sage, Thousand Oaks CA. URL: https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Gonzalez-Altozano, P., Castel, J.R., 1999. Regulated deficit irrigation in 'clementina de nules' citrus trees. I. yield and fruit quality effects. J. Hortic. Sci. Biotechnol. 74, 706–713. https://doi.org/10.1080/14620316.1999.11511177.

Green, S.R., Clothier, B.E., 1995. Root water uptake by kiwifruit vines following partial wetting of the root zone. Plant Soil 173, 317–328. https://doi.org/10.1007/BF00011470.

Green, S., Clothier, B., Jardine, B., 2003. Theory and practical application of heat pulse to measure sap flow. Agron. J. 95, 1371. https://doi.org/10.2134/agronj2003.1371.

Green, S., Clothier, B., Perie, E., 2009. A re-analysis of heat pulse theory across a wide range of sap flows. Acta Hortic. 846, 95–104. https://doi.org/10.17660/ActaHortic.2009.846.8.

Grossiord, C., Sevanto, S., Borrego, I., Chan, A.M., Collins, A.D., Dickman, L.T., Hudson, P.J., McBranch, N., Michaletz, S.T., Pockman, W.T., Ryan, M., Vilagrosa, A., McDowell, N.G., 2017. Tree water dynamics in a drying and warming world. Plant Cell Environ. 40, 1861–1873. https://doi.org/10.1111/pce.12991.

Grossiord, C., Sevanto, S., Limousin, J.M., Meir, P., Mencuccini, M., Pangle, R.E., Pockman, W.T., Salmon, Y., Zweifel, R., McDowell, N.G., 2018. Manipulative experiments demonstrate how long-term soil moisture changes alter controls of plant water use. Environ. Exp. Bot. 152, 19–27. https://doi.org/10.1016/j.envexpbot.2017.12.010.

Hernandez-Santana, V., Rodriguez-Dominguez, C.M., Sebastian-Azcona, J., Perez-Romero, L.F., Diaz-Espejo, A., 2023. Role of hydraulic traits in stomatal regulation of transpiration under different vapour pressure deficits across five mediterranean tree crops. J. Exp. Bot. 74, 4597–4612. https://doi.org/10.1093/jxb/erad157.

Huang, X.M., Huang, H.B., Gao, F.F., 2000. The growth potential generated in citrus fruit under water stress and its relevant mechanisms. Sci. Hortic. 83, 227–240. https://doi.org/10.1016/s0304-4238(99)00083-7.

Hutton, R.J., Loveys, B.R., 2011. A partial root zone drying irrigation strategy for citrus—Effects on water use efficiency and fruit characteristics. Agric. Water. Manage 98 (10), 1485–1496. https://doi.org/10.1016/j.agwat.2011.04.010.

Kassambara, A., 2023. ggpubr: 'ggplot2' Based publication ready plots. URL: https://CRAN.R-project.org/package=ggpubr. r package version 0.6.0.

Lalonde, D., Tegeder, M., Throne-holst, M., Frommer, W.B., Patrick, J.W., 2003. Phloem loading and unloading of sugars and amino acids. Plant Cell Environ. 26, 37–53. https://doi.org/10.1046/j.1365-3040.2003.00847.x.

Litvak, E., McCarthy, H.R., Pataki, D.E., 2012. Transpiration sensitivity of urban trees in a semi-arid climate is constrained by xylem vulnerability to cavitation. Tree Physiol. 32, 373–388. https://doi.org/10.1093/treephys/tps015.

Miller, S.A., Smith, G.S., Boldingh, H.L., Johansson, A., 1998. Effects of water stress on fruit quality attributes of kiwifruit. Ann. Bot. 81, 73–81. https://doi.org/10.1006/anbo.1997.0537.

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.

Morandi, B., Manfrini, L., Losciale, P., Zibordi, M., Corelli Grappadelli, L., 2010. Changes in vascular and transpiration flows affect the seasonal and daily growth of kiwifruit (*Actinidia deliciosa*) berry. Ann. Bot. 105, 913–923. https://doi.org/10.1093/aob/mcq070.

Morandi, B., Manfrini, L., Zibordi, M., Noferini, M., Fiori, G., Grappadelli, L.C., 2007. A low-cost device for accurate and continuous measurements of fruit diameter. HortScience 42, 1380–1382. https://doi.org/10.21273/HORTSCI.42.6.1380.

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.

Oren, R., Sperry, J.S., Katul, G.G., Pataki, D.E., Ewers, B.E., Phillips, N., Schäfer, K.V.R., 1999. Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. Plant Cell Environ. 22, 1515–1526. https://doi.org/10.1046/j.1365-3040.1999.00513.x.

Padilla-Díaz, C.M., Rodriguez-Dominguez, C.M., Hernandez-Santana, V., Perez-Martin, A., Fernández, J.E., 2016. Scheduling regulated deficit irrigation in a hedgerow olive orchard from leaf turgor pressure related measurements. Agric. Water. Manage 164, 28–37. https://doi.org/10.1016/j.agwat.2015.08.002.

Padilla-Díaz, C.M., Rodriguez-Dominguez, C.M., Hernandez-Santana, V., Perez-Martin, A., Fernandes, R.D.M., Montero, A., García, J.M., Fernández, J.E., 2018. Water status, gas exchange and crop performance in a super high density olive orchard under deficit irrigation scheduled from leaf turgor measurements. Agric. Water. Manage 202, 241–252. https://doi.org/10.1016/j.agwat.2018.01.011.

Patrick, J.W., 1990. Sieve element unloading: cellular pathway, mechanism and control. Physiol. Plant 78, 298–308. https://doi.org/10.1111/j.1399-3054.1990.tb02095.x.

Patrick, J.W., 1997. Phloem unloading: sieve element unloading and post-sieve element transport. Annu. Rev. Plant Physiol. Plant Mol. Biol. 48, 191–222. https://doi.org/10.1146/annurev.arplant.48.1.191.

R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/.

Romero, P., Navarro, J.M., Perez-Perez, J., Garcia-Sanchez, F., Gomez-Gomez, A., Porras, I., Martinez, V., Botia, P., 2006. Deficit irrigation and rootstock: their effects on water relations, vegetative development, yield, fruit quality and mineral nutrition of clemenules mandarin. Tree Physiol. 26, 1537–1548. https://doi.org/10.1093/treephys/26.12.1537.

Saliendra, N.Z., Sperry, J.S., Comstock, J.P., 1995. Influence of leaf water status on stomatal response to humidity, hydraulic conductance, and soil drought in *Betula occidentalis*. Planta 196, 357–366. https://doi.org/10.1007/BF00201396.

Torres-Ruiz, J.M., Perulli, G.D., Manfrini, L., Zibordi, M., Lopez Velasco, G., Anconelli, S., Pierpaoli, E., Corelli-Grappadelli, L., Morandi, B., 2016. Time of irrigation affects vine water relations and the daily patterns of leaf gas exchanges and vascular flows to kiwifruit (actinidia deliciosa chev.). Agric. Water. Manage 166, 101–110. https://doi.org/10.1016/j.agwat.2015.12.012.

Vandegehuchte, M.W., Steppe, K., 2013. Sap-flux density measurement methods: working principles and applicability. Funct. Plant Biol. 40 (3), 213. https://doi.org/10.1071/fp12233.

Wickham, H., 2016. ggplot2: Elegant Graphics For Data Analysis. Springer-Verlag, New York. URL: https://ggplot2.tidyverse.org.

Wickham, H., François, R., Henry, L., Müller, K., Vaughan, D., 2023a. dplyr: A grammar of data manipulation. URL: https://CRAN.R-project.org/package=dplyr. r package version 1.1.1.

Wickham, H., Vaughan, D., Girlich, M., 2023b tidyr: Tidy Messy Data. URL: https://CRAN.R-project.org/package=tidyr. r package version 1.3.0.

Zheng, S., Jiang, S., Cui, N., Zhao, L., Gong, D., Wang, Y., Wu, Z., Liu, Q., 2023. Deficit drip irrigation improves kiwifruit quality and water productivity under rain-shelter cultivation in the humid area of south China. Agric. Water. Manage 289, 108530. https://doi.org/10.1016/j.agwat.2023.108530.