Kiwifruit plant physiological behavior to different levels of soil water depletion under semi-arid environmental conditions

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Abstract

Kiwifruit crop is known to be extremely sensitive to unbalanced soil water content, both excess and deficit, and irrigation is therefore a key factor to be properly managed. A field experiment was conducted in a commercial kiwifruit orchard (*Actinidia chinensis* var. *chinensis* 'Zesy 002') located in Metaponto (southern Italy) to evaluate the variation of vine water status, leaf transpiration and stomatal conductance under different water deficit levels, by increasing depletion of soil water content in the top soil layers (0-35 cm). Reduced soil water availability was achieved gradually, by imposing an irrigation treatment of water restriction (70% of full crop requirements, ET_c) for a limited period of the growing season (15 days), which was monitored by multi-profile soil moisture probes. Stem water potential (Ψ), leaf transpiration (E) and stomatal conductance (gsw) were evaluated during the water stress phase and the subsequent recovery phase (7 days) and compared to the control, in which irrigation supply was aimed at ensuring the soil water content in the volume of soil affected by irrigation remained between the field capacity (FC) and the lower readily available water (RAW) level. Leaf transpiration and gsw decreased during the water stress phase, reaching minimum values at midday approximately 60 and 70% lower compared to control. Stem water potential became more negative due to the reduction in the soil water content, showing midday values of -14 bars at the end of the water stress phase. The prompt decline in E in response to Ψ lowering, occurring in the first days after the change in irrigation volumes, confirms a high sensitivity of kiwifruit vines to water deficit. During the recovery phase, a quick re-establishment of Ψ and a slow restoration of leaf activity and functionality were observed, making these parameters important indicators of the vine physiological status.

Keywords: plant water status, stomatal conductance, soil available water thresholds, transpiration, water stress

INTRODUCTION

Water resource scarcity is a growing problem that requires careful and sustainable agricultural water management, through the optimization of irrigation scheduling and the increase of plant water use efficiency. At the same time, soil water content is the main soil physical factor which, if not properly controlled, leads to excess or drought water conditions, negatively affecting and limiting plant growth and productivity (Kirkham, 2014). Kiwifruit is a very important fruit crop in several countries, including Italy, where the complexity of orchard systems makes it necessary to continuously study and monitor environmental and soil parameters in order to define or adapt optimal management strategies. Kiwifruit are known to have a significant water requirement and a reduced tolerance to water deficit conditions, which exposes them to severe risk of cavitation, hydraulic failure and leaf desiccation when water stress occurs (Martínez-Vilalta and Garcia-Forner, 2017; Bardi et al., 2022). As a result, kiwifruit orchards water requirement (approximately 6000-7000 m^3 ha^{-1} according to cultivation areas) is often overestimated, bringing attention to the susceptibility of this species also to waterlogging and soil anoxic conditions (Smith et al., 1990; Reid et al., 1991). Water is then a key factor that needs to be properly managed to provide the best soil

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water content conditions for plant growth and ensure high orchard productivity. Previous research focused on the specific morphological and anatomical characteristics of kiwifruit which affect plant-water relations, hydraulic features and the response mechanisms to water shortage. Kiwifruit vines have numerous fibrous tiny roots concentrated in the top soil layers and few and large xylem vessels (Ferguson, 1984; Condon, 1992), which promote the movement of a huge amount of water from soil to leaves through the plant without any particular resistance (Dichio et al., 2013). Low resistance to water flow, high transpiration rates and large size of leaves, characterize kiwifruit as a water consumptive plant (Chartzoulakis et al., 1993) and make it very sensitive to high evaporative demands. Understanding the water movement through the soil-plant-atmosphere continuum, influenced by particular orchard conditions, is essential to investigate vine behavior to different soil water content levels, taking into account the physiological traits and responses of the plant, and to ensure an optimal orchard management. Most of the information on the water relations of kiwifruit and its behavior to water stress relate to *A. chinensis* var. *deliciosa* (Montanaro et al., 2007; Dichio et al., 2013), while less is known about *A. chinensis* var. *chinensis*. Yellow fleshed cultivars seem to be less tolerant to water shortage compared to green cultivars, reaching stressed conditions with less negative stem water potentials (Black et al., 2012; Boini et al., 2022). On the contrary other studies found that *A. chinensis* var. *chinensis* has good stomatal control, which reduces transpiration if exposed to water stress (Mills et al., 2009). Considering conflicting reports, the behavior of *A. chinensis* var. *chinensis* under water restriction warrants further investigation. The present study aims at investigating at field scale kiwifruit vine water status and leaf activity and functionality under optimal and reduced irrigation and during a re-watering period. The analyzed physiological parameters contribute to increased knowledge about 'Zesy 002' (*A. chinensis* var. *chinensis*) water requirements in order to achieve optimal irrigation scheduling, suggesting wherever possible the adoption of water-saving or optimized irrigation strategies, increasingly needed, especially in Mediterranean environments characterized by water shortage.

MATERIALS AND METHODS

Study site description and experimental design

The experimental trial was carried out during the 2022 growing season in a commercial kiwifruit orchard (*A. chinensis* var. *chinensis* 'Zesy 002') located in Metaponto, southern Italy (40°24'46.32"N, 16°46'42.50"E). The yellow fleshed cultivar was grafted onto D1 rootstocks (*A. chinensis* var. *deliciosa*) in 2013 at 5×2 m spacing and trained as a pergola system. The physico-hydrological soil properties were evaluated to define the soil-water relation, in particular the quantity of water held at different values of soil matric potential, and therefore the threshold value of available water (AW) and the readily available water (RAW) fraction. Irrigation was provided by micro-sprinklers spaced 1 m from the trunk, with a flow rate of 40 L h^{-1} and a wetted radius of 0.90 m. All vines were grown under optimal water availability conditions during the irrigation season, which started at the end of April, until the beginning of the experimental trial. Daily vine water requirements were determined through the compilation of the theoretical water balance, using environmental data and crop coefficient (Kc) obtained from the FAO-56 guidelines. The scheduled irrigation volume was adjusted along the growing season, integrating information from a daily soil water balance of the soil volume wetted by irrigation with soil moisture sensors, in order to maintain the soil moisture level above the critical RAW threshold equal to 40% of AW for the kiwifruit orchard (Mininni et al., 2022). From August 23 onwards, irrigation volumes in 12 vines, distributed along a row, were reduced by 30% and adjusted taking into account rainfall contribution, in order to achieve a progressive soil water depletion. Two main plots were identified according to the irrigation treatment: control vines (C), where irrigation aimed at ensuring a soil water content level between the FC and the lower RAW level, water-stressed vines (WS), where irrigation was reduced for 15 days, with a gradual soil water content depletion. After the stress phase, vines were re-irrigated according to the irrigation strategy pursued during the growing season and kept for the control vines. Recovery phase monitoring lasted 7 days.

Meteorological data and volumetric soil water content monitoring

Environmental parameters, such as air temperature, relative humidity, solar radiation, rainfall and reference evapotranspiration were monitored from the AASD Pantanello weather station, which is located about 1 km from the experimental field. Air temperature and relative humidity recorded values were used to calculate the air vapor pressure deficit (VPD).

Frequency domain reflectometry (FDR) multi-profile soil moisture probes (Drill & Drop, Sentek Sensor Technologies Stepney, Australia) were used for constant monitoring of soil water content throughout the soil profile (15, 25 and 35 cm), allowing remote detection of instantaneous oscillations. Sensors were installed on the row at a distance of 0.5 m from the trunk and the micro-sprinkler.

Plant water status and leaf gas exchanges

Physiological measurements were performed during the stress phase (from August 23 to September 7) and the subsequent recovery phase (from September 8 to 14) to study vine behavior to increasing water deficit conditions and re-watering compared to control vines. Plant water status and stress level were monitored by measuring stem water potential (Ψ, bar) on six fully developed, expanded and exposed leaves chosen from three plants in each plot. The selected leaves were wrapped in a tin foil for about half an hour and then excised for immediate measurement with a Scholander pressure chamber (Model 1000, PMS Instrument Company, Corvallis, OR, USA) pressurized with nitrogen according to the procedure recommended by Turner (1981). The whole stem water potential daily trend was monitored on the last day of the stress phase (i.e., September 7) at two-hourly intervals throughout the day, from 5:30 (pre-dawn values) to 16:30 h, in order to verify synchronization of plant Ψ diurnal pattern, soil volumetric water content and VPD environmental conditions. Stomatal conductance (gsw, mol m^{-2} s^{-1}) and transpiration (E, mmol m^{-2} s^{-1}) were similarly monitored during the same day with a portable hand-held LI-600 porometer system integrated with a fluorometer (LI-COR Biosciences, Lincoln, USA). Values obtained were averages of six measurements taken on exposed leaves near the top of the canopy chosen from three vines in each plot. Ψ, gsw and E were measured across treatments between 12:00 and 13:00 h on four sunny days during the trial, two days for each phase.

Statistical analysis

Statistical differences among the two irrigation treatments were evaluated using RStudio statistical software. Data were subjected to an analysis of variance (one-way ANOVA) after testing for normality distribution (Shapiro-Wilk test) and homogeneity of variance (Barlett test) and calculations of least significant difference (LSD test) options were used to separate mean at each measurement day.

RESULTS AND DISCUSSION

Soil water content monitoring

For control vines, water availability in the first 35 cm soil depth was kept around the average value of approximately 40% (v/v) during the experimental trial, ensuring an optimal soil water content ranging between the value of FC and the established RAW threshold. Otherwise, soil water content in the plot subjected to water restriction gradually decreased, lowering by approximately 40% at 15 cm of soil depth and 20% at 25 and 35 cm of soil depth compared with control plot at the end of the stress phase (Figure 1). The occurrence of plant stress was quite immediate due to the reduced irrigation but, at the same time, limited by high soil water storage capacity that provides for the filling of deeper soil layers, which were not affected during the experimental trial (data not shown). Soil water depletion in the topsoil was sufficient to induce stress in plants due to the peculiar kiwifruit root system structure and characteristics which show a high root density and an intense development of thin feeder roots in the upper soil layers, affected by increased difficulty of water extraction. Taking into account root system structure and its spatial distribution is of great importance for optimizing water distribution and absorption, in order to prevent water stress phenomena or, conversely, waterlogging conditions.

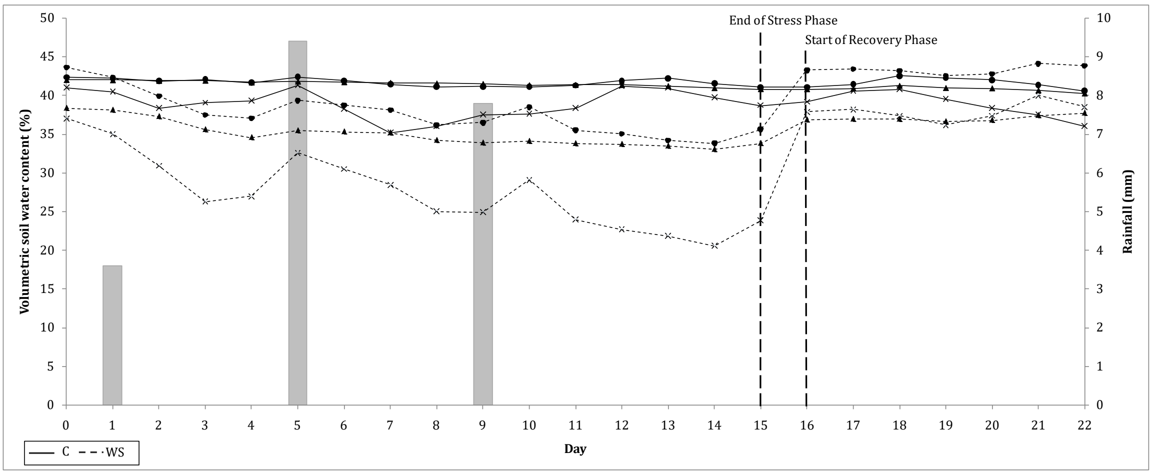

Figure 1. Soil water content trends monitored at 15 (×), 25 (●) and 35 (▲) cm of soil depth in the Control (C) and Water-Stressed (WS) plots. Grey bars represent daily rainfall.

Physiological responses

Stem water potential diurnal oscillations followed the daily trend in VPD (Figure 2A). Daily Ψ trend of control vines monitored on September 7 reflected the typical daily pattern, showing an almost sinusoidal curve (Sellin, 1999) where Ψ gradually decreased from a high value in the early morning to more negative value about midday, at higher evaporative demand, and then raised again in the afternoon (Figure 2A). These slight fluctuations throughout the day are typical of woody liana species, such as kiwifruit, due to the characteristic larger conducting vessels with perforated transverse walls, which promote the water movement and transport, and, in turn, establish a lower hydrostatic gradient between leaves and roots (Gucci et al., 1996; Dichio et al., 2013). Specific anatomical and morphological traits make kiwifruit particularly exposed to possible damages induced by water shortage. Daily Ψ trend of stressed vines monitored on the same day showed more negative potentials reaching values of approximately -14 bar. Moreover, at the last daily measurement point Ψ remained similar to midday values, indicating a compromised condition of the plant water status that required more time to recover compared to control vines (Figure 2A). Pre-dawn values (Ψ_{PD}) of plant water potential are usually used as the primary indicator of water stress (Judd et al., 1989). The lowering of the pre-dawn stem water potential of water-stressed compared to control vines indicated the inability of plants to restore, during nighttime hours, the water reserves in different tissues partially ceded to the transpiration flow during the day, due to soil water shortage. Once pre-dawn values of water-stressed vines dropped below ordinary values, mid-day readings fell dramatically below the range measured on well-irrigated vines, considering that the specific values depend on the particular days evaporative demand expressed by VPD. A depletion of approximately 20% (v/v) of the soil water content at 25 cm of depth resulted in a lowering of the Ψ_{PD} by -3.6 bar in stressed vines compared to those well-watered (Figure 2A). At the same time, physiological measurements showed a reduction of about 70 and 60%, respectively, in gsw and E of stressed vines compared with control vines during midday on the last day of water stress phase (Figure 2B, C). Differences in gsw and E between the two irrigation treatments were lower early in the morning, due to the stressed vines' exploitation of water reserves accumulated during the night, reaching the maximum differences in the interval from 10 to 14 h. Transpiration in stressed vines was considerably limited, relocating small amounts of water from the reserves of different tissues to the transpiration flow, trying to keep their water content high throughout the day.

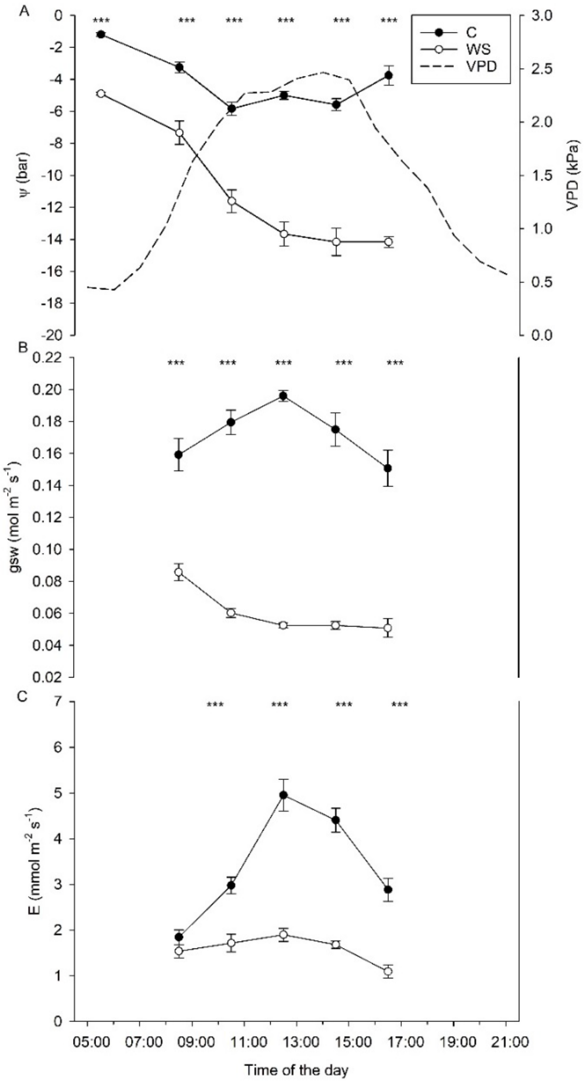

Figure 2. Daily changes in vapor pressure deficit (VPD) and stem water potential (Ψ) (A), stomatal conductance (gsw) (B) and transpiration rate (E) (C) in kiwifruit vines under two irrigation regimes, well-irrigated (♦) and water-stressed (□), during the last day of the stress phase (i.e., September 7). The differences between two means assessed by one-way ANOVA test are indicated at time of the day, *** ($P<0.001$). Values represented are the mean±standard errors (*n*=6).

The recovery phase began by supplying full irrigation (100% of full crop requirement, ET_C) to vines that were subjected to water restriction for 15 days with the aim of evaluating the time needed for kiwifruit to recover from the water stress level achieved. After rescheduling the irrigation of stressed vines, Ψ increased immediately, restoring values to those of the well-watered control vines within 24 h and then remained identical (Table 1), suggesting a rapid recovery of plant water potential in agreement with previous studies (Judd et al., 1989; Gucci et al., 1996; Montanaro et al., 2007). Water shortage negatively affected gas exchanges showing that gsw was the most sensitive physiological parameter to water stress. On day 10 and day 15 after the beginning of water restriction, gsw of stressed vines was respectively approximately 55 and 30% of that of irrigated vines. Recovery of gas exchange parameters upon re-watering depended on the level of stress reached during the specific drought period (Gucci et al., 1996). In contrast to Ψ, gsw showed a slow rate of recovery in agreement with Montanaro et al. (2007), reaching values of 90% of those of control vines 7 days after re-watering. Stomatal regulation of leaf gas exchanges is known to be an important process involved in tolerance mechanisms to drought, although it implies lower plant carbon gain due to reduced photosynthetic activity caused by stomatal closure. Stomatal conductance was sharply diminished with Ψ lowering, furthermore, stomata behavior was sensitive to changes in soil water content, according to Gucci et al. (1996). Therefore, *A. chinensis* var. *chinensis* 'Zesy 002' seems to have good stomatal control, limiting transpiration and water losses, in accordance with the results obtained on another yellow-fleshed cultivar (Mills et al., (2009).

Table 1. Comparison of midday stomatal conductance (gsw), transpiration (E), stem water potential (Ψ) and soil water content (SWC) in four days of the experiment, two for each phase (10 and 15 during stress phase; 16 and 22 during recovery phase) under two irrigation treatments.

Day	Treatment	gsw (mol m^{-2} s^{-1})	E (mmol m^{-2} s^{-1})	Ψ (-bar)	SWC (%)
10	C	0.18±0.01 a	3.99±0.21 a	-4.20±0.20 a	39.38
	WS	0.10±0.01 b	2.79±0.20 b	-5.90±0.37 b	33.76
	Significance	***	**	**	
15	C	0.20 a	4.95±0.35 a	-5.00±0.32 a	39.87
	WS	0.05 b	1.90±0.14 b	-13.50±0.94 b	29.72
	Significance	***	***	***	
16	C	0.21±0.01 a	4.40±0.24 a	-5.80±0.37 a	40.10
	WS	0.10±0.01 b	2.73±0.24 b	-5.60±0.24 a	40.54
	Significance	***	***	ns	
22	C	0.19±0.01 a	4.28±0.22 a	-6.8±0.20 a	38.28
	WS	0.16±0.01 b	4.02±0.25 a	-6.6±0.37 a	41.15
	Significance	**	ns	ns	

Data are mean values±standard errors (*n*=6). Different letters within columns indicate a statistical difference. **(P<0.01), *** (P<0.001), ns no significant difference.

CONCLUSIONS

Soil water content is a key factor as it influences plant growth, either directly or indirectly, as well as photosynthesis and transpiration rate, since both are mainly turgor-dependent processes, affecting also stomata behavior. The present study aimed to evaluate the effects of changes in soil water content on plant water status and physiological parameters, investigating the overall vine behavior to several soil water conditions. Anatomical and morphological characteristics of kiwifruit, such as root system distribution and plant hydraulic properties, influence plant-water relationships contributing to define vine behavior. Stem water potential and gsw in *A. chinensis* var. *chinensis* appeared to be sensitive to soil water status, as the progressive depletion of soil water content in the upper layers induced a decrease in both parameters due to the shallow rooting depth and the consequent reduced root capacity to absorb water, which caused hydraulic impairments related to water stress. Integrating knowledge about the processes triggered by water scarcity conditions is pivotal to improve irrigation strategy and management, especially in semi-arid environmental conditions, which are constantly exacerbated by the current climate change crisis, and increase awareness of water resource value and importance in particular for kiwifruit cultivation.

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