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Apple trees' behavior to a single-season megadrought stress

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Abstract

Extreme weather events such as megadroughts (long duration and intense droughts) are becoming common in regions with Mediterranean climates and threaten the continuity of fruit production. In this context, this study assesses the effects of a single-season megadrought on the physiological response and mortality of mature apple trees in a high-density orchard. Two treatments were imposed in two weighing lysimeters with four trees in each one, (i) Control: fully irrigated according to the crop evapotranspiration; and (ii) Drought: rainfed from 7 May 2023, until the end of the season. Trees' evapotranspiration and trunk water potential were continuously monitored during the experiment in combination with periodic measurements of the soil water content, stomatal conductance, midday stem water potential, and apple size. The trunk water potential of apple trees in the drought lysimeter during the 2023 season fell below −4.5 MPa, with stomatal conductance decreasing from 0.4 mmol m^{-2} s^{-1} before withholding irrigation to 0 mmol m^{-2} s^{-1} 60 days later. In the following spring 2024, the four apple trees subjected to the megadrought were agronomically dead (did not sprout). Our results showed that, for apple trees, a threshold value of water potential of -3.5 MPa must not be surpassed to ensure the tree survival, while values below −4.0 MPa for 27 days cause the death of the trees.

Introduction

Apples are the most cultivated fruits in Europe with an annual production higher than 12.6 million tons (EUROSTAT 2024). Apple trees (*Malus domestica* Borkh.) adapt to a great variety of edaphoclimatic conditions, with water availability being a critical factor for optimal tree development and fruit production (Landsberg and Jones 1981). Adequate soil water availability ensures that apple trees can photosynthesize, transpire, transport nutrients and photosynthates throughout the tree, regulate canopy temperature, and maintain turgor pressure within their cells to grow and produce fruit.

In recent years, due to climate change and the shift in the precipitation pattern, European apple-producing countries such as Italy, France, and Spain (top 2, 3, and 5 largest producers) have experienced how an increase in the intensity and frequency of extreme droughts represents a challenge for growing high-quality apples (Grillakis 2019). In this sense, in 2023, Catalonia, the main apple-productive region in Spain, experienced a record-breaking extreme drought. The scenario was so dramatic that water for agriculture was expected to be reduced by 80%, and one of the major irrigation districts in Catalonia, the Canal d'Urgell, planned to cut the irrigation season off due to a lack of water resources in April for the first time in its 160-year history, leaving 50,000 ha of irrigated crops without water. Had that been the case, fruit production would have been impossible and tree survival would have been threatened. Fortunately, that was not the case. However, this situation highlighted the dependency on water availability of the Catalan apple productive sector. Other fruit-producing regions in the world, such as the Central Valley and the Southern region of California (Liu et al. 2022), the Western Cape Province of South Africa (Theron et al. 2023), the Central Regions of Chile (Muñoz et al. 2020) or the Kashmir Valley of India (Ahmed et al. 2019) have also experienced and are projected to suffer similar extreme droughts again, commonly called megadrought (Cook et al. 2022).

Megadroughts lead to uncontrolled water stress that affects tree physiological, vegetative, and reproductive responses, decreasing stomatal conductance, transpiration, and carbon assimilation, and prioritizing survival mechanisms over tree

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and fruit growth (Lopez et al. 2012). Moreover, it should be considered that apart from the immediate effects that water deficits cause on the physiological and agronomical responses while they are happening, extreme droughts also cause carryover effects during the next seasons even if the trees are not under water restrictions and increase the vulnerability of the trees to disease and pest infestations (Kannenberg et al. 2020). When extreme droughts are excessively long and intense, they might lead to a tree hydraulic failure, impeding water movement from roots to leaves (loss of hydraulic conductivity), affecting carbon and nutrient allocation, causing leaf wilting and drop as well as xylem cavitation, and in the last place the potential dieback of the tree (Trugman et al. 2018).

For apples, many studies have characterized and studied the physiological and agronomical responses of apple trees to controlled soil water deficits and have proposed, and assessed irrigation strategies considering scenarios of limited water resources achieving water savings that ranged between 50 and 80% of the water applied to a fully irrigated tree (Fallahi et al. 2010; Girona et al. 2010; Lo Bianco and Francaviglia 2012; Neilsen et al. 2016; O'Connell and Goodwin 20072007). The deficit irrigation strategies reported in those works agreed that severe water stress reduced tree vegetative growth, apple yield, and quality (primarily size). These strategies planned a continuous distribution of irrigation water throughout the season, which in a scenario of severe water restriction (megadrought) might not be possible. Few studies have reported the effects of a severe drought (no irrigation) on irrigated field-grown fruit trees. For almond trees, Moldero et al. (2022) reported that 92% of the trees submitted to severe irrigation restrictions for one season in Cordoba (Spain) eventually died. For peach trees, Proebsting and Middleton (1980) reported that 31% of the trees died after one season of no irrigation in Washington State (USA). However, for apple trees, Ebel et al. (2001) reported that after one season without irrigation in Washington State (USA), no tree died or showed shoot die-back the next season. According to these studies, apple orchards might be viewed as highly resistant to megadroughts compared to other fruit orchards. However, factors such as the soil texture and depth, which strongly influence soil water availability for the tree and root development and distribution, and the environmental conditions (rainfall and atmospheric demand) that condition crop evapotranspiration play a crucial role in enhancing or mitigating the effects of the water deficit on the tree water status. Moreover, apple orchards have changed greatly in the last decades and that conclusion might not be right under current conditions. The adoption of dwarfing rootstocks with limited root growth and narrow training systems that maximize light interception allowed apple orchards to move from a traditional low-density system (<500 trees ha^{-1}) with furrow irrigation, to a modern high-density drip-irrigated system (>2000 trees ha^{-1}). Consequently, there is no information on the physiological response of modern field-grown apple orchards under water deprivation conditions and their adaptative mechanisms to cope with water scarcity and avoid drought-induced mortality. Information quantifying how severe water stress affects tree water consumption and its physiological and agronomical responses is important to understand the limits of tolerance of apple trees to water stress. Moreover, identifying threshold values for soil and plant water status indicators after which if maintained or exceeded trees will die, will help growers determine a no-return point to manage their apple orchard under severe irrigation water restrictions and adopt effective management practices to mitigate these effects and ensure the continuity of apple orchards after a megadrought.

The present experiment aimed to characterize the effects of severe irrigation limitations caused by a megadrought on the physiological and agronomical response of mature apple trees, emphasizing the impact on the evolution of tree's water relations and tree mortality, in order to determine the no-return point from which the tree will die.

Materials and methods

Experimental plot

The experiment was carried out during the 2023 season (from 7 May to 31 August). The experimental plot was located at the IRTA Mollerussa Experimental Field Station in Lleida, Spain (41°37'N, 0°52'E; 260 meters above sea level). It consists of a 1 ha apple orchard (*Malus domestica* Borkh. cv 'Golden Reinders'), planted in 2011 with a spacing of 3.63 m by 1.20 m in a north-south row orientation. The apple trees were grafted onto 'M.9' rootstock and trained to a modified central-leader system. The irrigation system consisted of a double drip line per tree row with four emitters per tree of 3 L h^{-1}.

Two weighing lysimeters were installed at the center of the experimental plot (Girona et al. 2011). Each lysimeter has a surface area of 9.6 m² and holds 4 apple trees, representing a total area of 17.424 m² of the planted orchard. The lysimeters are located 200 m apart from each other. A schematic presentation of the lysimetric station is provided by Girona et al. (2004).

Experimental approach

To evaluate the differential behavior of well-irrigated orchard trees and non-irrigated ones, irrigation water supply to one of the apple lysimeters (the one located on the east side) was completely halted on 7 May 2023 and remained so until the beginning of September 2023. The only water this lysimeter received was from rainfall. Consequently, this lysimeter began to dry out, simulating a drought condition (L-Drought), while the other lysimeter continued to be fully irrigated (L-Control). L-Control was daily irrigated during the whole season to satisfy tree water requirements (evapotranspiration) based on the weight changes registered by the lysimeter following the usual irrigation practices for these lysimeters (Girona et al. 2011).

Measurements and controls

Environmental parameters such as reference evapotranspiration (ET_0) and rainfall (daily and hourly), were collected from the "Mollerussa" weather station owned by the Servei Meterologic de Catalunya, located 40 m away from the orchard plot. ET_0 was calculated according to Allen et al. (1998) and directly derived from the original Penman-Monteith equation for a reference crop (grass with 0.12 m height).

Crop Evapotranspiration (ET_C) was determined by measuring the weight loss reported for each lysimeter and dividing it by the planted area (17.424 m²). The lysimeters are configured to record a weight value every minute, allowing for the analysis of the daily pattern of weight loss or ET_C.

One microtensiometer sensor (FP; FloraPulse, Davis, CA, USA, www.florapulse.com) was installed in each of the 8 lysimeter trees (4 trees per lysimeter) to determine trunk water potential (Ψtrunk) (Blanco and Kalcsits 2021, 2023; Lakso et al. 2022).

Eight neutron probe access tubes were installed in each lysimeter following the same pattern to characterize the soil water content at different distances from the irrigation line and the tree trunk. Volumetric soil water content in these access tubes was monitored using a neutron probe (Hydroprobe 503DR, Campbell Pacific Nuclear Corp., Martinez, CA, USA), which had been previously calibrated for this site (Douglass 1966). Measurements were taken at depths between 0.20 and 1.40 m, at 20 cm intervals.

Midday stem water potential (Ψstem, MPa) was measured on two leaves per tree, eight leaves in each lysimeter, at solar noon (13:00–14:00, GMT+2), using a pressure chamber (Soil Moisture Equipment Corp., Model 3000, Santa Barbara, CA, USA) as recommended by Turner (1988). Selected leaves were fully expanded, healthy, located on the shaded side of the tree, close to the trunk, and covered with black polyethylene and aluminum foil for at least 30 min before measurements (McCutchan and Shackel 1992). Likewise, and at the same time, the stomatal conductance was measured. To assess stomatal conductance of apple trees, two leaves per tree, eight leaves per treatment, were measured using a portable porometer (Li-600, LI-COR Biosciences, Lincoln, NE, USA). Measurements were taken on sunlit, fully expanded, healthy leaves located at mid-canopy height. Physiological measurements were conducted on clear, sunny days to ensure consistent light conditions.

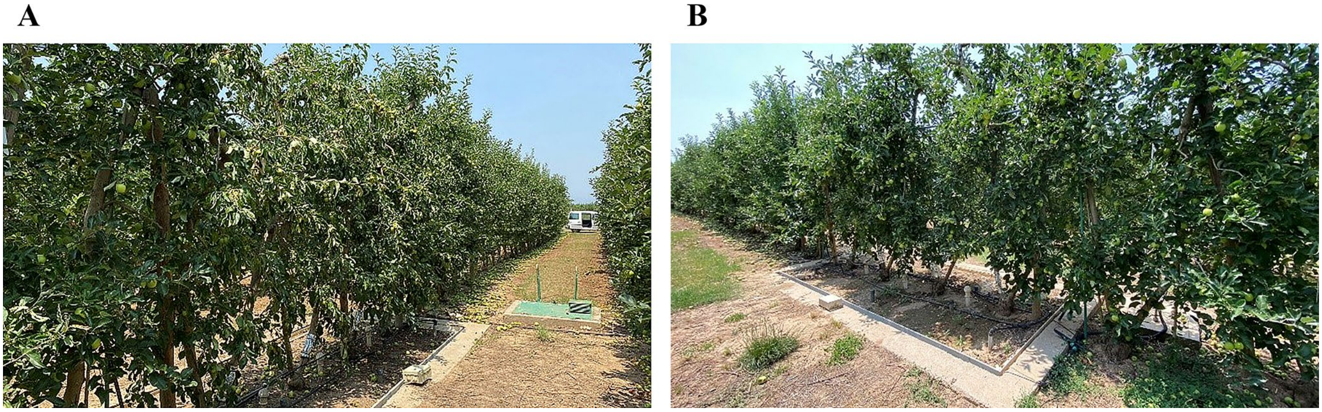
Crop load was adjusted by hand thinning, following commercial practices, to one apple per cluster and a separation among fruits of at least 15 cm (Gonzalez et al. 2024), reaching a final average crop of 250 fruits per tree at harvest. To assess the impact of different irrigation treatments on apple growth, we conducted detailed samplings and measurements of fruit fresh and dry mass in the laboratory. From each lysimeter, a representative sample of 6 apples was periodically collected during the season (nine times). The apples were selected randomly from various sections of the tree to ensure a representative sample of the entire canopy. Apples were cold stored and transported to the laboratory immediately after sampling to assess fruit fresh mass, preventing any moisture losses. Dry mass was evaluated after placing the apples in a drying oven set at 62 °C until they reached a constant mass.

Results

Visual signatures of drought stress

From the beginning of the experiment until the end, some pictures were taken for both lysimeters (L-Control and L-Drought). Initially, the trees from both lysimeters were in perfect shape (Picture 1, 1 May 2023; DOY 121), however, during the evolution of the experiment, the apple trees under severe water deficit (L-Drought) showed visual symptoms of how the imposed megadrought affected the trees' normal development and behavior. On 27 June 2023, (DOY 178), 51 days after the water withholding in L-Drought, the Drought trees had visual features that indicated that the trees were deeply stressed (Picture 2 A) such as flagging leaves, while the Control trees had well-developed canopies with functional leaves (Picture 2B). On 19 July 2023, (DOY 200), 73 days after the water withholding in L-Drought, the leaves of the Drought trees although they remained green, began to wilt (Picture 3). On 5 August 2023 (DOY 217), 90 days after the water withholding in L-Drought, the whole canopy of the Drought trees consisted of wilted grayish-green leaves at the start of the senescence while the oldest leaves were completely dried and had already turned brown (Picture 4). At the end of the experiment, on 1 September 2023 (DOY 244), 117 days after the water withholding in L-Drought, all the leaves in the Drought trees were dry (dead-brown) and the apples on the tree were small and dehydrated (Picture

Picture 1 Drought Lysimeter (31 May 2023)



Picture 2 **A**: Drought Lysimeter and **B**: Control Lysimeter (27 June 2023)

5 A). On the other hand, for the same date, Control trees were completely active with healthy transpiring leaves (green) and commercial-sized apples (Picture 5B).

The visual effects of the imposed megadrought on the apple trees were also noticeable the following season. The severe water deficit imposed on the Drought trees in 2023 had a carry-over effect the next season as none of the four apple trees contained in the L-Drought bloomed the next spring and only three trees erratically sprouted a small number of buds located in the lower part of the trunk of the trees. There were no buds that sprouted in the section of the tree above 1 m from the grafting point, consequently, more than two-thirds of the total height of the trees had no leaves which indicated that the severe water deficit to which the Droughts trees were subjected caused their agronomic death (Picture 6, 17 May 2024; DOY 138).

Evapotranspiration

The accumulated daily ET_0 for the experimental period was 581.8 mm and ranged between 2 and 6.5 mm day^{-1}, while for the same period the accumulated precipitation was 158.5 mm. ET_0 followed the traditional seasonal pattern of Mediterranean regions with warm springs and hot summers, with maximum daily values above 6 mm during July and August (Fig. 1). Daily ET_C of Control apple trees followed a similar pattern to that of ET_0 with an accumulated ET_C for the season of 504.6 mm which corresponded to 87% of the

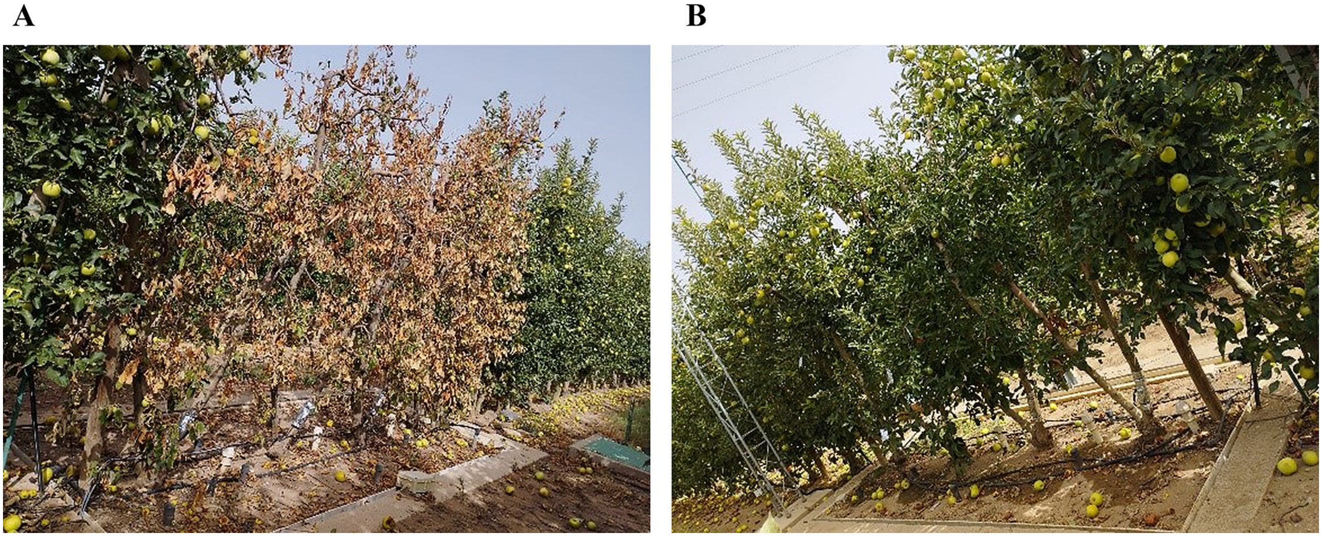
Picture 3 Drought Lysimeter (19 July 2023)

Picture 4 Drought Lysimeter (5 August 2023)

ET_0. ET_C of Control trees rose from bud-break when it had values that ranged between 2 and 4 mm day^{-1}, and were lower than ET_0 by 30%, to reach similar values to those of ET_0 (6.5 mm day^{-1}) when the canopy was completely developed. For Drought apple trees, the accumulated ET_C was 168.9 mm, and the daily ET_C evolved from values similar to those of the Control trees (4 mm day^{-1}) before the irrigation withholding (May 7th, 2023) to values close to 0 mm at harvest (the end of the experiment - September 1st, 2023) when the trees had no active leaves (Fig. 1).

Soil water content

Volumetric soil water content reflected the two different scenarios imposed on each lysimeter (Fig. 2). L-Control had mean values of soil water content that ranged between 13.5 and 16% for the whole season, indicating that Control trees were not under relevant water restrictions. Soil water content in L-Drought, although the season started with similar mean values to those of the L-Control (16%) rapidly decreased to 12% (20 days after the irrigation withholding) (Fig. 2). Regarding the distribution of the water in



Picture 5 **A**: Drought Lysimeter and **B**: Control Lysimeter (1 September 2023)

Picture 6 Drought Lysimeter (Following Season, 17 May 2024)

the soil profile of L-Drought, despite showing a consistent decrease throughout the evolution of the experiment, the pattern of soil water content at different depths was stable (Fig. 3). For all the depths, 50% of the total water content in the L-Drought was depleted in the first 40 days after the irrigation cut-off, and 90% after 78 days (DOY 205; 24 July 2023). On the other hand, in the L-Control, soil water content remained stable with values of high soil water content (14–18%) at the region between 10 and 40 cm depth where the roots were located and even increased at deeper depths (Fig. 3).

Tree water status

Changes in soil water content affected tree water status. Ψstem was a reliable tree water status indicator that rapidly reflected differences between treatments once the water withholding was imposed on the Drought trees. For Control trees, the variability of Ψstem during the season (from −1.0 to -1.5 MPa) was attributed to changes in the environmental conditions, with the lowest values on dates with the highest vapor pressure deficit (Fig. 4). For Drought apple trees, Ψstem rapidly decreased from values of -0.8 MPa to -1.8 MPa in the first ten days after irrigation was withheld, and after 50 days of drought, it fell to -3.5 MPa (Fig. 4). The water input to the L-Drought from the rain events partially recovered the tree water status or slowed down the fall of the Ψstem in Drought trees. After the second rain episode (50 mm, DOY 180; 29 June 2023), Ψstem increased from −3.3 MPa to -1.6 MPa. However, in less than 10 days after the rain episode, Drought trees again had Ψstem values below −2.5 MPa. After the third rain episode (20 mm,

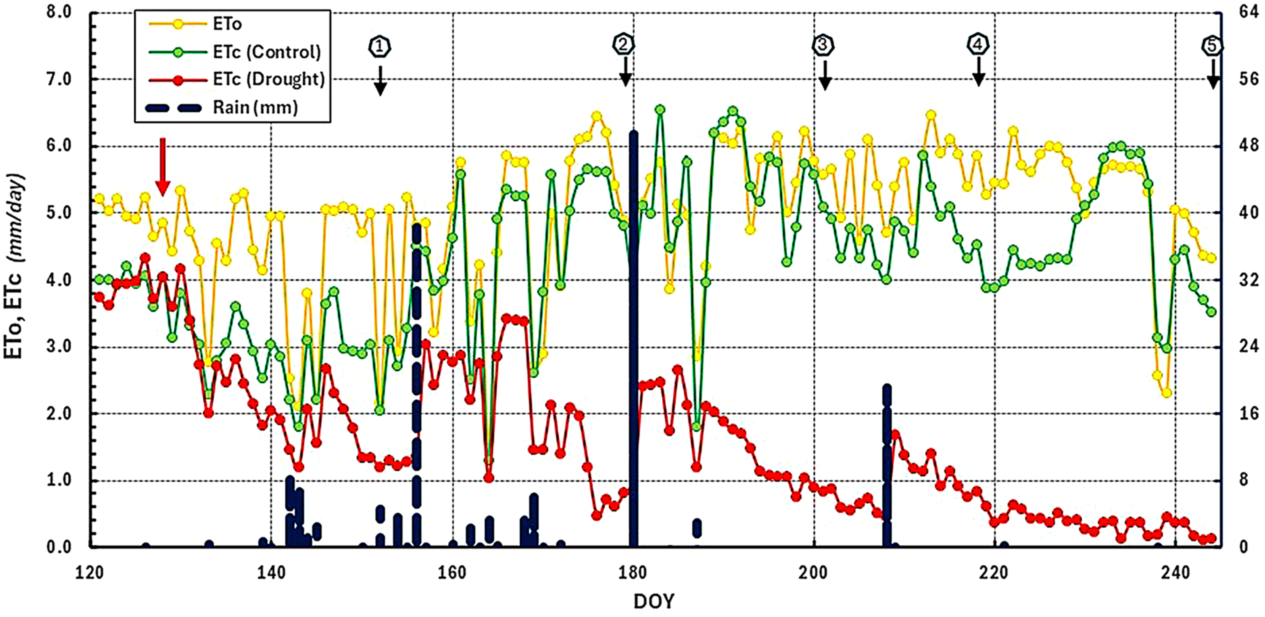


Fig. 1 Seasonal evolution of the Reference Evapotranspiration (ETo), Crop Evapotranspiration (ETc) of the trees in the Control (green) and Drought (red) lysimeters and cumulative daily rain for the 2023 experimental period (from May to September). ETo and rain data comes from the weather station close to the experimental field and ETc from the two weighing lysimeters. The red arrow indicates when irrigation was cut off on the Drought Lysimeter, and the heptagons correspond to the pictures: 1 (31 May 2023), 2 (27 June 2023), 3 (19 July 2023), 4 (5 August 2023) and 5 (1 September 2023)

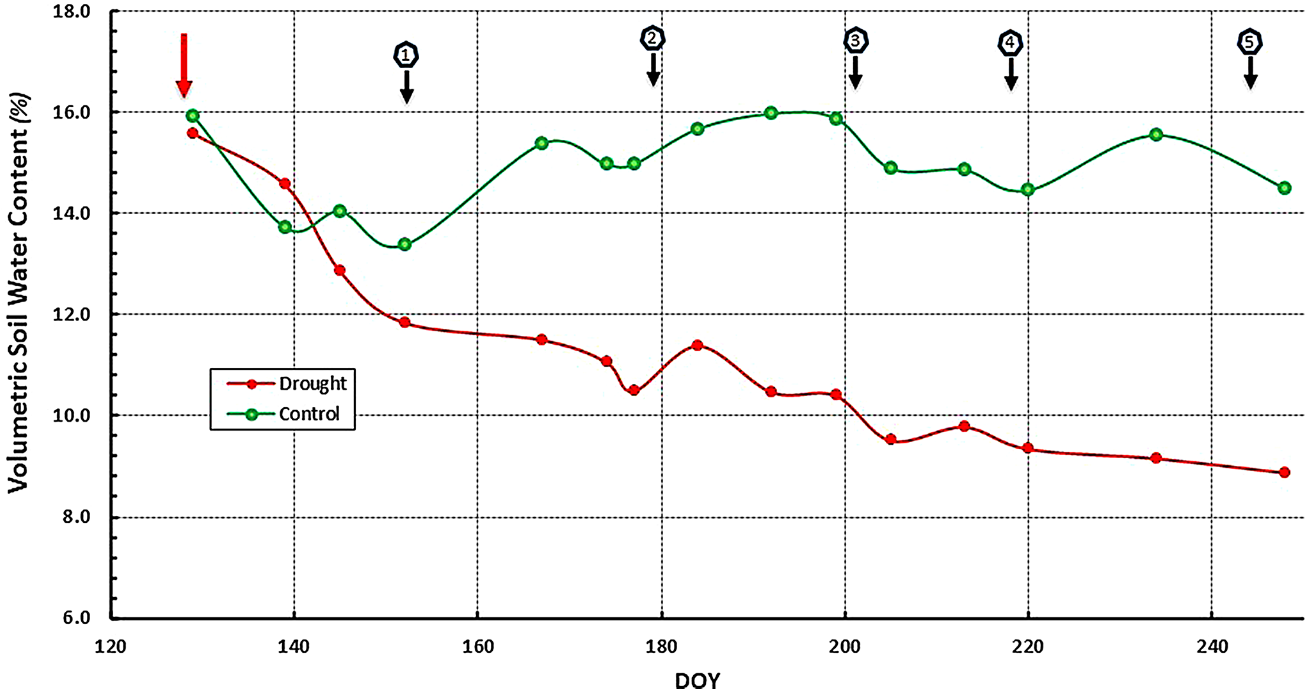


Fig. 2 Volumetric soil water content (%) seasonal evolution for 2023 experimental period (from May to September). Each dot represents the average of 56 values (8 neutron probe access tubes and 7 depths in each tube). The red arrow indicates when irrigation was cut off on the Drought Lysimeter, and the heptagons correspond to the pictures: 1 (31 May 2023), 2 (27 June 2023), 3 (19 July 2023), 4 (5 August 2023) and 5 (1 September 2023)

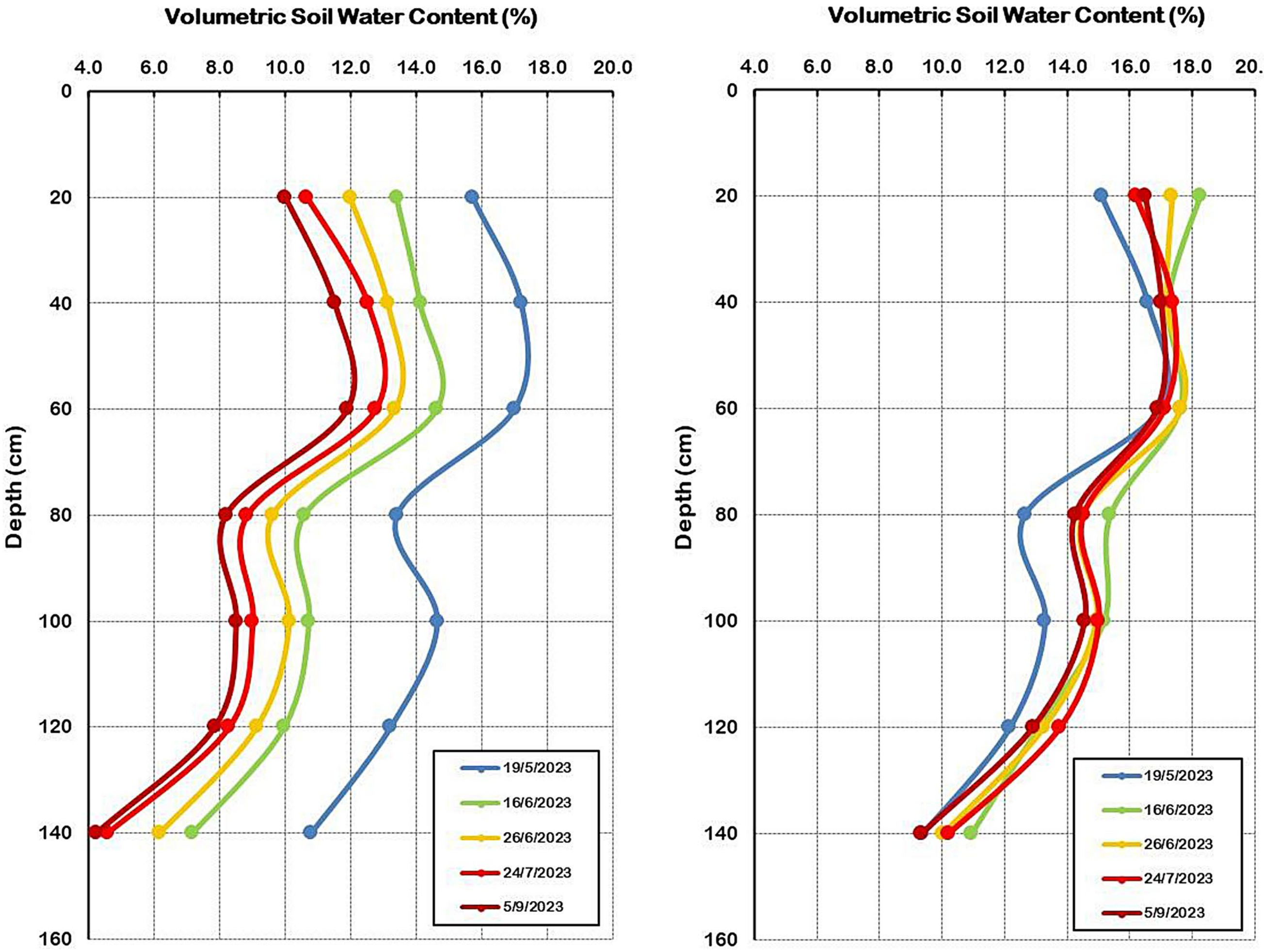


Fig. 3 Volumetric soil water content (%) profiles for five specific dates on each Lysimeter (Left: Drought; Right: Control) for the 2023 experimental period (from May to September). Each dot represents the average of 8 values (8 neutron probe access tubes)

DOY 208; 27 July 2023), the Ψstem increased from −3.5 to -2.6 MPa, however, five days later it fell below −3.5 MPa. From this point onwards the severe drought stress caused a decline of the Ψstem to values similar to -3.5 MPa for several days and the defoliation of the Drought trees. Values of Ψstem reported in this study as -3.7 MPa in the Drought trees were lower as they could not be measured due to limitations with the Scholander pressure chamber used, as it had a maximum operating pressure of -3.5 MPa. The stomatal conductance was also very responsive to the tree water status. Control trees had stomatal conductance values that indicated that the trees were not submitted to a megadrought (0.3–0.5 mol m^{-2} s^{-1}), and similarly to the Ψstem, the variability of these values could be related to the changes in the environmental conditions (Fig. 5). On the other hand, Drought trees decreased their stomatal conductance mirroring the soil water content from values similar to the Control trees (0.4 mol m^{-2} s^{-1}) to the total stomata closure 60 days after the irrigation withholding and remained in values close to 0 mol m^{-2} s^{-1} until the end of the season while the leaves were wilting. Moreover, the stomatal conductance of the Drought trees did not show any permanent recovery after the rain episodes (Fig. 5).

Once the Drought trees had no functional leaves, the traditional measures of Ψstem on covered leaves with the Scholander pressure chamber and the stomatal conductance were impossible to do, however, the tree water status of the trees was still continuously monitored by measuring Ψtrunk with the microtensiometers. Thus, Ψtrunk was strongly related to Ψstem and both indicators showed similar values for both treatments during the season (Fig. 6). This relationship proved the reliability of the Ψtrunk measured by the FP microtensiometers to assess the tree water status of apple trees. Control trees' daily minimum Ψtrunk ranged between −0.8 and −2.0 MPa (Fig. 7). For the Drought trees, Ψtrunk followed the same pattern as Ψstem. It decreased as the soil water content depleted and increased after the rain events, however, at the end of the experiment (DOY 220–8 August 2023 - and onwards) when the leaves of the canopy were wilting because of the severe drought, their

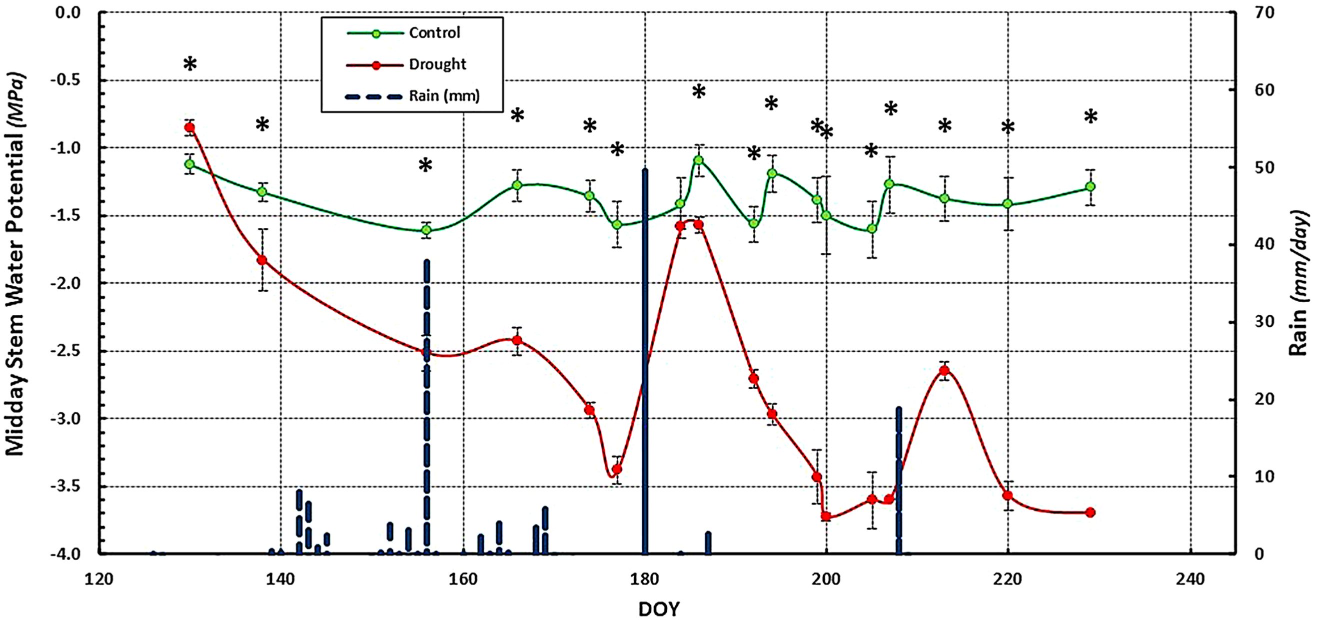


Fig. 4 Seasonal evolution of the Midday Stem Water Potential for the trees in the Control (green) and Drought (red) Lysimeters and cumulative daily rain for the 2023 experimental period (from May to September). Each dot is the average of 8 stem water potential measurements ± 1.5 StdError. (*) Significant treatment differences ($P<0.05$, LSD). Values of -3.7 MPa could be lower because the used plant water status console had a measurement limit of -3.7 MPa. After DOY 230 there were no leaves to measure on the Drought Lysimeter

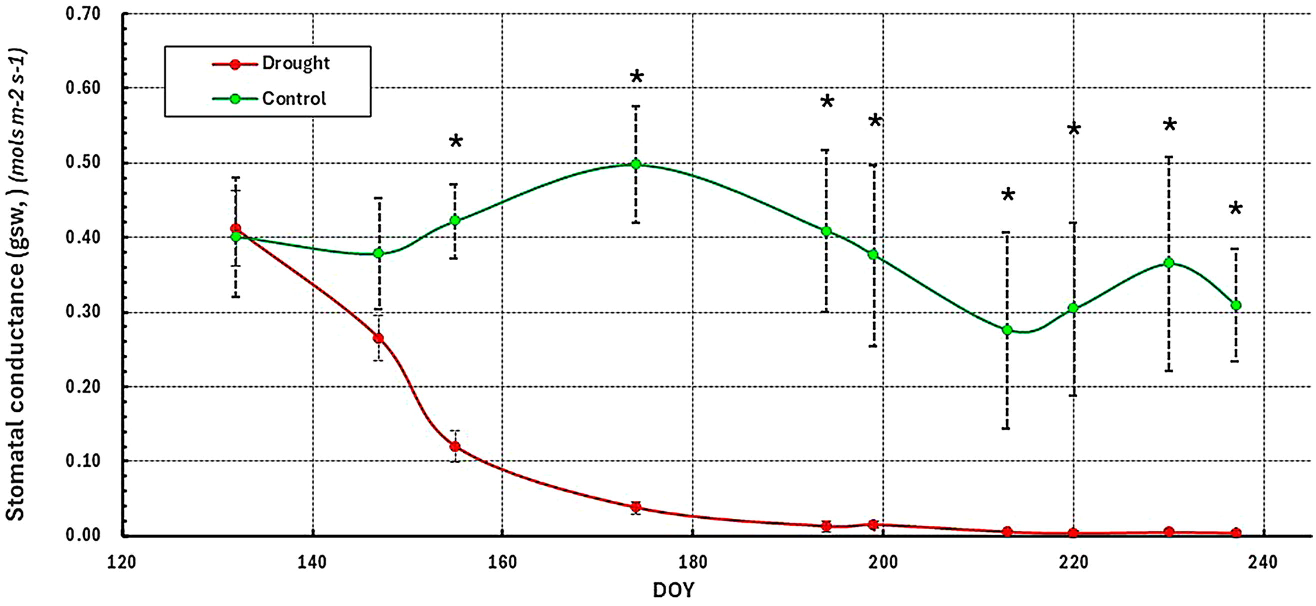


Fig. 5 Stomatal conductance seasonal evolution for the 2023 experimental period (from May to September) for the apple trees in the Control (green) and Drought (red) Lysimeters. Each dot is the average of 8 measurements ± 1.5 StdError. (*) Significant differences between treatments ($P<0.05$, LSD)

stomatal conductance values were similar to 0 mol m^{-2} s^{-1} and values of Ψstem were not possible to be measured due to limitations with the console (Ψstem < -3.7 MPa), Ψtrunk of the Drought trees decreased to values close to -5.0 MPa (Fig. 7).

Fruit growth

The enormous differences reported in the water status of the apple trees from the different treatments had a huge impact on fruit development and final fruit fresh mass (Picture 7). Figure 8 shows the trend of apple growth (dashed line) and

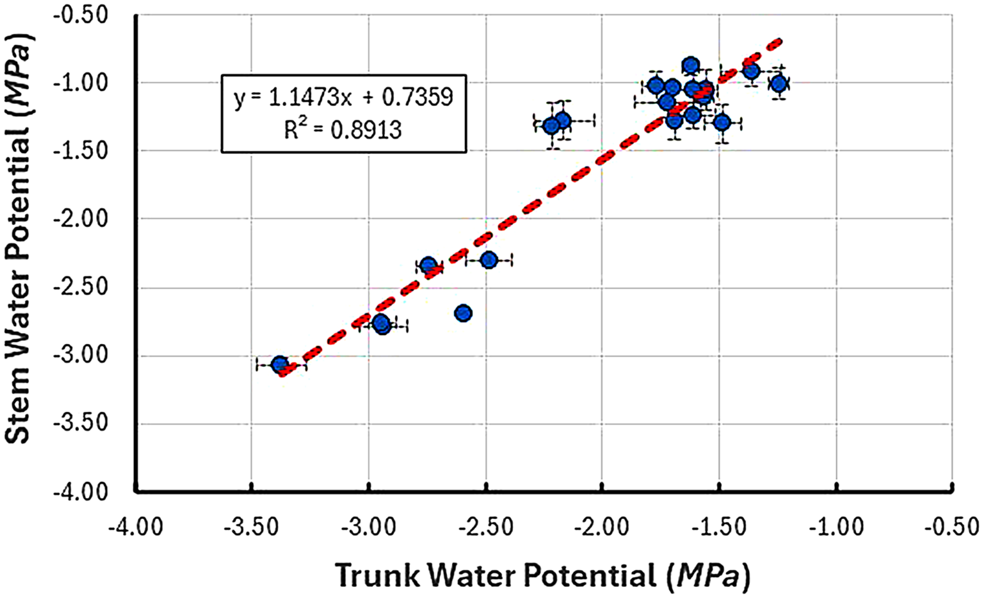


Fig. 6 Relationship between trunk water potential measured with the microtensiometers (FP sensors) and midday stem water potential measured with the pressure chamber. In all the cases, trunk potential values correspond to the time when stem potential was determined. Each point represents one treatment and day. The error bars of each point indicate the value of +- 1 Std Error for the stem water potential (horizontally) and the trunk water potential (vertically)

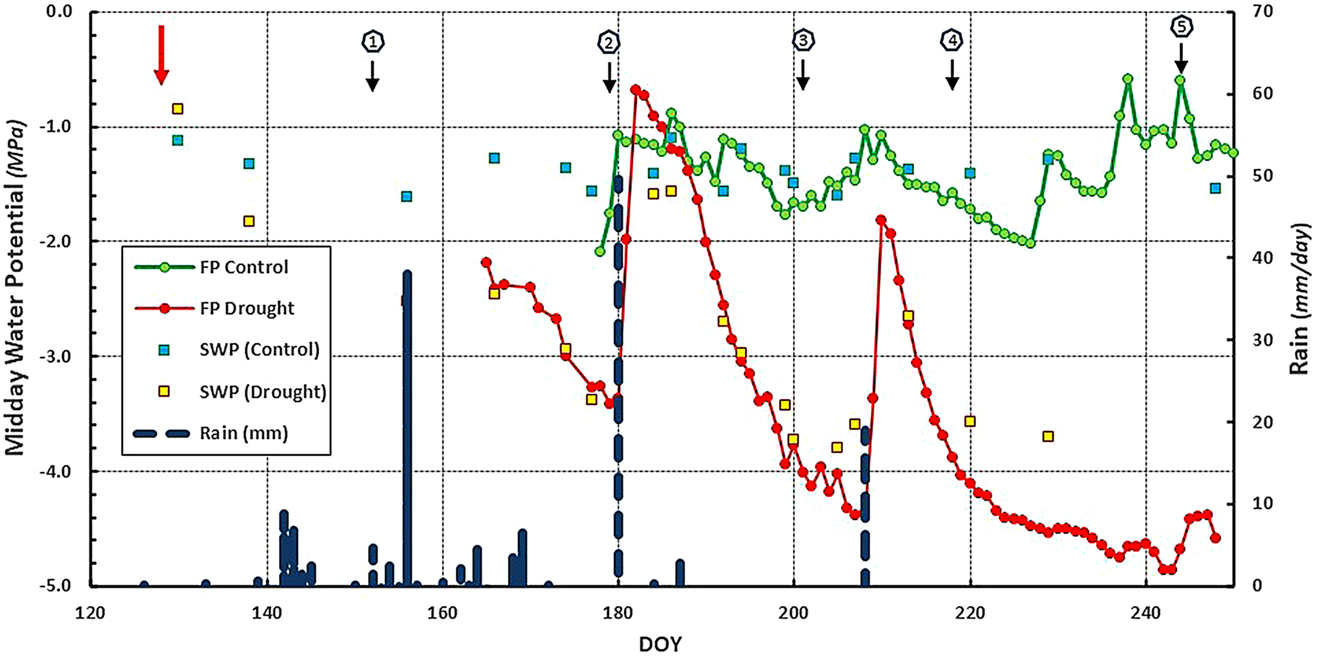
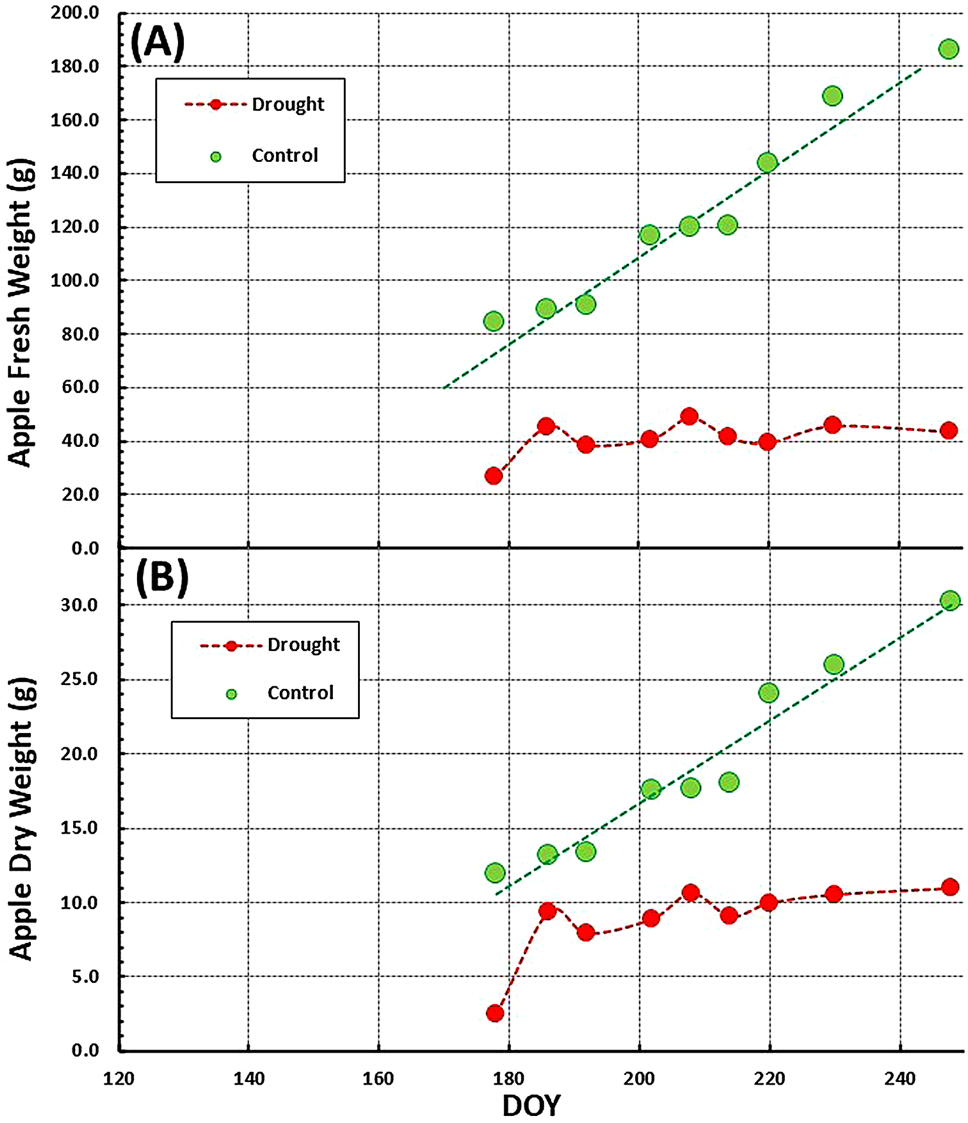


Fig. 7 Midday Water Potential seasonal patterns for Trunk Water Potential measured with the FloraPulse® sensors (FP) and for Stem Water Potential (SWP) measurements with the Scholander pressure chamber in both lysimeters Control and Drought for the 2023 experimental period (from May to September). The red arrow indicates when irrigation was cut off on the Drought Lysimeter, and the heptagons correspond to the pictures: 1 (31 May 2023), 2 (27 June 2023), 3 (19 July 2023), 4 (5 August 2023) and 5 (1 September 2023)

the measured values (circles) for both treatments. The stepwise pattern of fruit growth measured for the apples from the Control trees in Fig. 8 was due to the small number of fruits sampled ($n = 6$) to avoid an over-extraction and not disturb the crop load of the four trees of each lysimeter. Apples from Control trees showed a continuous increment of fresh and dry mass during the last stage of fruit growth (DOY 180–243; from 29 June to 31 August 2023). For this period, Control apples increased their fresh mass by more than 100 g (50% of the final fresh mass of the apples at harvest) and their dry mass by 20 g (66% of the final dry mass of the apple) reaching values of 200 g and 30 g for fresh and dry mass, respectively. For the apples from the Drought trees and for the same period, as a result of the severe drought that those trees were facing, they increased their fresh mass by 20 g and their dry mass by 8 g, ending the season with apples of 40 g of fresh mass which corresponded to 11 g of dry mass.

Picture 7 Fruit samples from Drought (left) and Control (right) Lysimeters on 27 June 2023

Fig. 8 Seasonal evolution of the fruit growth of the apples grown in the Control (green) and Drought (red) Lysimeters for the 2023 experimental period (from May to September). Each dot is the average of 4 apples. **A**) apple fresh weight, **B**) apple dry weight



Discussion

As expected, once the irrigation was restricted in the L-Drought, the soil water content decreased and the daily ET_C of Drought trees dropped. This response indicated the rapid reduction in the transpiration of irrigated apple trees when they faced severe water restrictions which confirmed the hypothesis of the work of the high susceptibility of modern high-density apple orchards, formed by trees grafted on dwarfing rootstocks, to severe droughts. In this sense, Cohen and Naor (2002) and Olien and Lakso (1986) reported for the cultivars 'Golden Smoothee' and 'Empire', respectively, that those trees grafted onto dwarfing rootstocks (M.9) had significantly lower transpiration, stomatal conductance, and leaf-specific hydraulic conductance for the first cultivar and lower Ψstem for the second, compared to those grafted on more vigorous rootstocks (MM.106). These results might indicate that droughts and demanding environmental conditions impact more those trees with dwarfing rootstocks and small rooting volume than those vigorous rootstocks that allow a vast distribution of the roots in the soil, and promote a higher root: shoot ratio. In this study, the fast decrease of the ET_C of the Drought trees can be explained by the phenological stage of the tree when the drought happened and the environmental conditions (high ET_0 and vapor pressure deficit), as these factors exacerbate the effects of water deficit (Nalevanková et al. 2020). Summer droughts, such as the one imposed in the present study, that match highly demanding days and the phenological stage of the trees when their canopy is fully developed and the fruits are important sinks of water and carbohydrates, have been reported to cause the greatest suppression of tree transpiration (Li et al. 2023). Thus, ten days after the irrigation withholding the ET_C of Drought trees decreased by 25% compared to Control trees, and after 30 and 60 days without irrigation, the ET_C of the Drought trees declined by 33 and 66% compared to the Control trees, respectively. From that day onwards most of the leaves in the Drought trees were wilting and showed a total stomata closure. In accordance with that daily ET_C values, recorded by the weighing lysimeter (L-Drought), drastically decreased to values below 0.5 mm day^{-1}. The rapid response of the Drought trees to the irrigation cut-off decreasing their transpiration should be interpreted in the context of the trees being located in a lysimeter (a container) which might lead to a faster depletion of the soil water content and a quicker/stronger reaction to the water deficit compared with in-ground trees. On the other hand, it must be said that weighing lysimeters-based studies are one of the most accurate methodologies to measure tree evapotranspiration (Girona et al. 2011; Lorite et al. 2012; Yang et al. 2000) and study seasonal changes in tree transpiration comparable to those under field conditions. Thus, the evolution of ET_C reported in this study for both treatments confirmed that although total tree transpiration is the sum of the transpiration of all the organs of the tree (leaves, fruits, stems), it is mainly driven by leaf area (Jackson 2003), so for Drought apple trees when their leaves lost their functionality, although the other organs remained in the tree, the transpiration was negligible.

The changes in the ET_C recorded by the lysimeters for each water availability scenario (Control and Drought) were also in line with the changes in the tree water status measured at the tree and leave scales (Ψstem, Ψtrunk, and stomatal conductance). Ψstem and Ψtrunk were robust tree water status indicators for apple trees and once the soil water content in L-Drought decreased identified differences between treatments. For apple trees, several works have also reported the reliability of Ψstem to measure tree water status (De Swaef et al. 2009; Doltra et al. 2007; Wheeler et al. 2023). The values of Ψstem observed for Control trees, in the range between −1.0 and −1.5 MPa, have been traditionally reported for irrigated apple trees under no water deficit scenarios (Espinoza-Meza et al. 2023; Girona et al. 2010; Naor et al. 1995). The changes in Ψstem that Control trees showed were mainly influenced by the environmental conditions, following a similar seasonal pattern to that of the ET_C measured in the L-Control. For Drought trees, the values of Ψstem and Ψtrunk of -3.0 MPa reached after 45 days of water withholding indicated that they were under severe drought stress which if continued for the long term might cause a carryover effect on the physiological response of the trees the next season. In this sense, Girona et al. (2010) reported for 'Golden' apple trees that Ψstem values close to -2.5 MPa, although, they represent that the trees were under severe drought stress, that stress does not cause any detrimental effect on the following season. However, after a rain episode of 50 mm (DOY 180) their Ψstem and Ψtrunk returned to similar values to the Control trees. Nevertheless, 20 days after that rain episode and 70 days after the irrigation cut-off in the L-Drought, both indicators fell below −3.5 MPa, which pointed out the rapid decrease of Ψstem that the trees experienced after their recovery. Similarly, Auzmendi et al. (2011) reported for the apple combination 'Golden Smoothee'/M.9 that the trees submitted to two subsequent cycles of irrigation withholding and recovery had a faster drop of Ψstem the second cycle and a limited recovery of the stomatal conductance. In our experiment, once Drought trees reached the critical threshold of -3.5 MPa there were visual symptoms that the leaves began to wilt which was the mechanism that the tree had to reduce their functional leaf area and avoid excessive water loss by transpiration, slowing tree water potential decrease and, protecting against cavitation. This avoidance mechanism to cope with water stress has been analyzed by Wolfe et al. (2016) who reported this behavior of leaf wilting and shedding as the capacity of the leaves to act as 'hydraulic fuses' under severe drought scenarios. The threshold value of -3.5 MPa of Ψstem observed in this study agreed with the results previously published for 'Golden Delicious' apple trees relating it to the total stomatal closure of the leaves of the tree and a reduction of the hydraulic conductivity of the branches by 50% (Beikircher et al. 2013).

Stomatal regulation in apple trees has been reported to be highly responsive to environmental and soil conditions (Lakso 1994). In this regard, apple trees have been traditionally considered water-conservative trees, so when they face soil water restrictions or highly demanding atmospheric conditions, rapid partial stomata closure has been described as a characteristic mechanism for avoiding excessive negative Ψstem values (Jones 2004; Lauri et al. 2016). In this experiment, this behavior was observed in Control trees which had a fairly constant Ψstem during the season and, small decreases in soil water content or high evaporative demand triggered reductions in the stomatal conductance. On the other hand, for Drought trees, this behavior was not observed, and although there was a reduction of the stomatal conductance as a response to the severe soil water deficit, it did not prevent a great drop in the Ψstem and Ψtrunk. Avoiding a total stomata closure in trees under severe drought, despite decreasing their Ψstem to values that can promote embolism, is a strategy of the trees to optimize carbon gain (Breda et al. 2006; Zhao et al. 2023). Moreover, it was observed that the stomatal conductance was not as responsive as the Ψstem to rapid changes in soil water content, and when the leaves started to lose their functionality, it did not recover after any rain episodes. This response of Drought trees highlighted that the changes in Ψstem and Ψtrunk at that time, when the drought stress had already caused total stomatal closure and led to leaf wilting, were more related to the hydration of the xylem tissues of the tree than to a complete physiological recovery.

Several works have reported how sensitive apple growth is to water stress (Boini et al. 2019; Gonzalez-Nieto et al. 2023; Mpelasoka et al. 2001) and strong relationships between apple final fresh mass and the mean/accumulated water deficit that the trees experience during the season (Ebel et al. 2001; Girona et al. 2010; Naor et al. 2008). In our study, the low water potential and the stomatal closure measured in the Drought trees penalized fruit growth and caused carbon starvation, which harmed the final fresh and dry mass of the apples. Through the analysis of the evolution of the apple development, it was observed that after the second rain episode (DOY 180), when Ψstem increased from −3.3 to -1.6 MPa, the apples from the Drought trees exhibited the greatest increase in mass observed in the whole period. For the third rain episode, no growth was observed, indicating that the trees were not responsive to changes in the soil water content at that time. In apples, carbon assimilation is strongly related to stomatal closure (Lakso 1994), consequently, the reduced fruit growth measured on the apples from the Drought trees during the 60 days previous to harvest, the stage of cell enlargement, was presumably related to the total stomatal closure that Drought trees experienced.

Ψtrunk monitored by the microtensiometers has been reported for apple trees as a reliable tree water status indicator (Blanco and Kalcsits 2024; Lakso et al. 2022). In our study, it was the only tree water status indicator capable of quantifying drought stress at the tree level during the last part of the season when there were no functional leaves in the Drought trees. Thus, Ψtrunk reached values close to -5.0 MPa which have been reported by Beikircher et al. (2013) for 'Golden Delicious' apple trees as the threshold value for irreversible hydraulic failure, when the 88% of tree hydraulic conductivity is lost and it is more probable that under those conditions of severe drought stress, trees will die (Hammond et al. 2019; Urli et al. 2013). Moreover, we hypothesize according to our results for 'Golden Reinders', that the proposed threshold value of -5.0 MPa might be too negative and reaching values of Ψtrunk below −4.0 MPa for 27 consecutive days was enough to cause air-seeded xylem embolism and block water transportation through the upper part of the trunk and branches of the Drought trees which finally caused their death. The study of tree mortality and the determination of the lethal threshold of hydraulic failure caused by the occlusion of water transportation to perimeter branches of the tree are important to understand the physiological mechanism that trees have to face severe droughts and model tree die-off, as well as to assess the possible effects of severe droughts to woody perennials and know the limits of water deficit that trees can cope with before they die (Cochard et al. 1992; Sperry and Tyree 1988). To our understanding, the present work is the first report that characterizes the length and intensity of drought stress required to induce hydraulic failure and the death of mature apple trees and relates them with daily values of tree water potential and evapotranspiration.

The non-returning threshold value of Ψtrunk proposed in this study for the apple combination 'Golden Reinders'/M.9 of -3.5 MPa was slightly less negative than the one proposed by Moldero et al. (2022) of -4.0 MPa of Ψstem for almond trees under megadrought conditions. Almond trees at that level of water deficit completely defoliated that season and 92% of them were dead the next season (they did not sprout). For peach trees under no irrigation for one season, Proebsting and Middleton (1980) could not state a non-returning threshold value which would lead to the tree's death. However, they stated that the limit might be in the range between −2.6 and −3.9 MPa of leaf water potential, as it caused the defoliation of 60–80% of their canopy and the death of 31% of the trees. Moreover, and despite the high variability that they reported in tree water status within the same orchard, they observed that all the peach trees whose leaf water potential was below −3.0 MPa, if they survived the next season, did not produce any fruits. Regarding other works in apple trees, Ebel et al. (2001) reported for the combinations of apples 'Delicious'/M.7 and 'Delicious'/MM.111 after one season without irrigation, values of Ψstem below −2.5 MPa for the whole experiment with two days in mid-summer with values below −3.5 MPa. The drought stress reported in that study, although it was not as strong as the one measured in our study, provoked leaf shedding which reduced total tree leaf area by 60 to 35% at harvest, reduced vegetative growth and fruit fresh mass, but it did not cause the death of the trees. These results agree with those reported in the present study in which we can state that values of Ψtrunk below −3.5 MPa severely penalize apple tree agronomic response, as it reduces vegetative development and decreases fruit growth as an early mechanism to cope with water deficit, and if the deficit persists or intensifies promotes leaf shedding and finally the death of the tree.

Conclusion

In summary, we conclude that −3.5 MPa of Ψstem and Ψtrunk is a reliable threshold value for apple orchards that should not be surpassed to avoid carry-over effects that could jeopardize tree survival. Moreover, values of water potential below −4.0 MPa maintained for 27 days during the preharvest will surely kill the trees.

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Declarations

Competing interests The authors declare no competing interests.

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