Water stress during the post-harvest period affects new root formation but not starch concentration and content in Chardonnay grapevine (*Vitis vinifera* L.) perennial organs

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Abstract

Water stress responses during the post-harvest period were evaluated in a Chardonnay container-grown grapevines grafted onto 1103 Paulsen rootstock. The irrigation treatments were: a control treatment (C) (irrigated to match ET_C demands) and a water stress treatment (WS) (irrigated when midday stem water potential reached a -1.1 MPa threshold). Photosynthesis, biomass and carbohydrate content were determined on five vines in each treatment on specific dates, from harvest until leaf fall. Stressed vines reduced leaf area due to defoliation, while well-watered vines had a higher carbon accumulation allowing the formation of new roots during the post-harvest period. No dry biomass accumulation was observed in the shoot and trunk organs after fruit harvest. Starch concentration and content were not affected by water stress. At the end of the experiment, starch concentrations were lower in the shoots and trunk than in the roots. Water stress induced a variation on biomass accumulation between above and below ground perennial organs, with the roots being the main organs in which biomass and starch concentrations were accumulated and kept, respectively.

Keywords

Leaf area, leaf net assimilation rate, reserve organs, stem water potential

1. Introduction

Water stress can be a limiting factor in perennial crops, affecting important physiological processes such as photosynthesis and respiration (Chaves et al. 2010). Plant growth depends on the carbon balance which, in turn, is linked to photosynthesis and the respiration balance and is often limited by water availability (Flexas et al. 2006). As a result, numerous studies have focused on plant responses to water stress during the vegetative growth period, with the grapevine providing a clear example (*Vitis vinifera* L.) (Girona et al. 2009, Rogiers et al. 2011).

The grapevine has its origin in the Mediterranean basin and its growth cycle has adapted to the climatic condition in this area (Terral et al. 2010). Grape production in the regions surrounding the Mediterranean basin is an important activity, occupying approximately 2,768,000 hectares (OIV 2017). In such regions, the onset of vegetative growth is defined by bud break (Duchêne et al. 2010). It takes place during spring and is accompanied by a significant mobilization of carbohydrates from plant reserves. This permits new vegetative growth until leaves reach 50 % of their final size to become net carbon exporters (Vaillant-Gaveau et al. 2014, Köse and Ates 2017). Depending on the grapevine cultivar, this mobilization of reserves may even be extended almost until anthesis (Zapata et al. 2003). The accumulation of carbohydrates during the previous season is therefore essential for sustaining the mobilization of reserves until photosynthesis becomes the main source of carbon in spring (Zapata et al. 2004, Smith and Holzapfel 2009).

The accumulation of carbohydrates in storage tissues depends on total photosynthesis and the partitioning of carbon among different plant organs (Howell 2001, Smith and Holzapfel 2009). In temperate climate vines, several studies have demonstrated that the majority of the carbohydrate restoration in storage tissues takes place during the post-harvest period, which supports vine reserve recovery (Bennett et al. 2005, Vaillant-Gaveau et al. 2014). Although the rate of photosynthetic activity decreases in line with leaf senescence (Bertamini and Nedunchezhian 2003), functional leaves remain active and help the replenishment of reserves (Scholefield et al. 1978, Loescher et al. 1990). Even in areas with short post-harvest periods, carbohydrate pool replenishment tends to be sufficient to maintain yield levels (Bennett et al. 2005, Vaillant-Gaveau et al. 2014). In most grape-growing regions, vines retain their leaves after harvest (Bennett et al. 2005). However, the length of time that leaves are retained on the vine and the effectiveness of their photosynthetic activity depend on the cultivar, climatic conditions and viticultural practices (Williams 1996, Trought et al. 2011, Hall et al. 2016).

Starch is the primary reserve form for carbohydrates stored in trunk and root organs (Mullins et al. 1992, Pellegrino et al. 2014, Köse and Ates 2017). Although starch concentration seems to be influenced by grapevine cultivar, climate and vine management (Bennett et al. 2005), the majority of starch storage is located in roots (Bates et al. 2002, Zapata et al. 2004). The root system consists of: coarse roots, which provide a structural framework, anchorage, transport and storage for carbohydrates, and nutrients for the woody organs; and fine roots, which are generally responsible for water and nutrient uptake (Comas et al. 2010). Root development in grapevines has been described as cyclical, with two main flushes of growth: in spring, between several days after bud break and bloom; and in autumn, between harvest and leaf fall (Mullins et al. 1992, Tomasi 2016). Root growth is an energy-dependent process involving endogenous sink-source relations which depend on the availability and partitioning of carbohydrates. The main environmental factors regulating root growth are soil temperature (Kaspar and Bland 1992, Rogiers et al. 2013, Clarke et al. 2015) and water availability. The latter has been described as the most important factor regulating root growth and development (Eapen et al. 2005, Tomasi 2016). However, the impact of water stress on carbon accumulation following harvest has so far received relatively little attention. Furthermore, compared with the above-ground organs (such as leaves, shoots and trunk organs), there are few studies of root processes in grapevines (Field et al. 2009, de Herralde et al. 2010, Holzapfel and Smith 2012, Miranda et al. 2017). This is probably because these types of studies are highly time consuming and, to the best of our knowledge, at certain specific points in the post-harvest period (Bates et al. 2002); this is usually an overlooked period for grapevines (Hall et al. 2016).

In Mediterranean climatic regions, the post-harvest period coincides with low evaporative demand and late summer rain events. As a result, numerous studies have focused on grapevine responses to water stress during the period of vine growth (spring-summer) in which the probability of heat or water stress is high (Eapen et al. 2005, Duchêne et al. 2010). However, according to climate projections, an increase in the frequency and intensity of the drought events is expected, not only throughout the growing cycle of the grapevines, but also during post-harvest (Gonçalves et al. 2014, Ramos et al. 2018). Under such a scenario, the aims of the present study were to compare the relative contributions of the shoot, trunk and root organs of Chardonnay grapevines to the restoration of carbohydrate reserves under well-watered and water stress conditions during the post-harvest period.

2. Materials and methods

2.1. Experimental site and plant material

The experiment was carried out at Raïmat (41º40'37'' N – 0º28'38'' E), Lleida (Catalonia, Spain), during 2015 and 2016. In spring 2015, 172 one-year-old Chardonnay grapevines that had been grafted onto 1103 Paulsen rootstock were planted in 50-L containers. The growing media consisted of loose stones at the bottom of each container and a substrate mix consisting of peat, sand and silty-loam soil, in equal parts. Disease control and nutrition management were performed according to the wine grape production protocol of the 'Costers del Segre' Denomination of Origin (Catalonia, Spain).

2.2. Experimental design, irrigation treatments and water applied

The vines were fully irrigated until the beginning of the experiment, using the crop reference evapotranspiration method (Allen et al. 1998). The post-harvest irrigation study started in late August 2016, after fruit harvest (August 25). For this study, 64 uniform vines were selected and arranged in two rows, of 32 vines each (with a separation between rows of 3 m). The container walls were painted white to prevent excessive root temperatures. The experiment was laid out in a complete randomized block design with two treatments and four replications of eight vines. The experimental unit consisted of eight vines (8 vines x 2 treatments x 4 replications).

Two irrigation treatments were applied: a control (C), scheduled to satisfy full water requirements (100% ET_C), and a water stress treatment (WS). In the latter, irrigation was triggered once the midday stem water potential (SWP) threshold of -1.1 MPa was reached, following Bellvert et al. (2016). The WS vines were scheduled to receive 50%, 15% and 10% of the ET_C, in August, September and October, respectively. The amount of water applied to each experimental unit was monitored using digital water meters (CZ2000-3 M, Contazara, Zaragoza, Spain).

2.3. Water status and net assimilation rate measurements

Midday stem water potential (SWP) and leaf net CO_2 assimilation rate (A_n) (µmol CO_2 m^{-2} s^{-1}) measurements were made once per week from post-harvest (August 26) until leaf fall (October 19), measuring one leaf of three of the eight vines per experimental unit in each replication and treatment. Midday stem water potential (SWP) was determined using a pressure chamber (3005-series portable plant water status console, Soil

Moisture Equipment Corp., Santa Barbara, California, USA) following the McCutchan and Shackel (1992) procedure. Measurements were made at solar noon on shaded leaves located close to the main trunk. Leaves were covered with plastic sheathes with aluminium foil bags for at least 1 hour before measurements were taken. Leaf net CO_2 assimilation rates were measured with an infrared gas analyser (model LCi; ADC BioScientific Ltd., Hoddesdon, Herts, UK). A portion of each leaf was placed in the chamber window area of 6.25 cm^2 and data were taken after 45 s, when the A_n reading had stabilized. All the measurements were taken in less than an hour. The integrated A_n reading for successive dates and for the whole experiment was calculated according to Basile et al. (2011), as follows:

$$\int A_n = \sum_i^{i+1} \left| \frac{A_{n\,i} + A_{n\,i+1}}{2} \cdot (t_{i+1} - t_i) \right| \quad (1)$$

Where A_n is the leaf net assimilation rate and t are the measurement days.

The integrated A_n ratio between irrigation treatments was determined as:

$$Ratio\ A_n = \int A_{n\,WS} / \int A_{n\,C} \quad (2)$$

Subscripts WS and C represent the water stress and control irrigation treatments, respectively.

2.4. Biomass determination

Vine biomass was sampled during the post-harvest period on the following dates: August 25 (initial date from which the differential irrigation treatments were applied), September 20, October 4, October 24 and November 28. The first sampling date was scheduled before the start of the irrigation treatment, when five vines were selected. For the following sampling dates, five vines were selected per treatment. The vines were split into above-ground organs (leaves, shoots and trunk) and below-ground organ (root system). Each above-ground organ was dried in a forced-air oven at 65ºC to constant weight and then the dry weight of each organ was recorded. Leaf area (LA) was measured on a subsample of 20 leaves from each vine, except on the last day, because by then, all the leaves had naturally fallen off the vine. Leaf areas were measured with a leaf area meter (Li-COR 3200; Li-COR, Lincoln, NE, USA). After the sub-samples were measured they were placed in a forced-air oven and dried to a constant weight. The resulting values were then related to the whole vine leaf dry weights to obtain LA measures for each vine.

The root system was washed in a container at the field, and subsequently classified, into 4 categories, in the lab: a) underground stem of the rootstock, b) thick roots (> 2 mm), c) fine roots (suberized), and d) new

roots (fine non-suberized). The differentiation between suberized and non-suberized fine roots was made by colour, as the new roots were lighter and finer, and the fine roots were darker (Clarke et al. 2015). The whole root system was dried and the dry weights were recorded as previously described for the above-ground organs. The proportion of new roots in relation to the total root system was expressed considering the severity and duration of the water stress effect, calculating the water stress integral from the SWP measurements for the period.

2.5. Starch accumulation

Vine starch concentration was determined in the shoots, trunk and thick roots (> 2 mm). For each vine, 12 g fresh weight samples were taken for the shoots and trunk and 10 g samples for the thick roots. These were frozen in liquid nitrogen and then dried in a forced-air oven at 65ºC. Once the dry weight was constant, the samples were ground using a hand mill (M20; IKA-WERKE, Staufen, Germany). Starch concentration determination was carried out using a polarimetry technique in line with European regulation CE 152/2009.

2.6. Statistical analysis

The effect of the irrigation treatment on leaf net CO_2 assimilation rate, organ dry mass and starch content were evaluated by a one-way ANOVA followed by a Tukey's significant difference test. The same analysis was carried out on the assessment of the effect of the sampling dates on starch concentration. All the statistical analyses were performed using R software (R Core Team 2017) (R version 3.2.4 Revised) and the statistical significance was established at $P<0.05$.

3. Results

3.1. Applied water, water status and net assimilation rate

Each vine received 237 L of water from bud break to harvest prior to the beginning of the experiment. Then, from harvest to leaf fall, the control (C) vines received 116 L per vine, whereas the water stress (WS) vines received 46 L per vine. During this period, the stem water potential (SWP) in the C vines ranged from -0.4 to -0.6 MPa (Figure 1). In the WS treatment, the aim was to subject the vines to moderate stress levels, with a threshold value of -1.1 MPa. The irrigation threshold was exceeded on two occasions: on September 13 (-1.2 MPa) (following a 2.9 mm late summer rain event typical of Mediterranean conditions); and at the end of the

experiment (-1.4 MPa), when the vine water status recovered to non-stress values, following a 21.6 mm rainfall event (Figure 1). Since the environmental conditions of the experiment were not favourable for achieving stress after October 19 in the WS vines (Figure 2), that date was taken as the end point of the differential irrigation management.

The water stress imposed in the WS treatment induced some early leaf fall in mid-September (Figure 3). Thereafter, the reduction in leaf area (LA) (m^2) was related to leaf senescence. In contrast, in the C treatment, only leaf senescence was responsible for reductions in LA (Figure 3).

The leaf net CO_2 assimilation rate (A_n) for the C treatment ranged from 5.9 to 10.6 µmol CO_2 m^{-2} s^{-1}, while that for WS was between 2.3 and 14.1 µmol CO_2 m^{-2} s^{-1} (Figure 4). From the onset of the experiment until September 22, the WS leaf net assimilation rates were below those of the C treatment; for the remainder of the period, those for WS were greater than for C (Figure 4). The relation between the integrated A_n of WS vines and C vines was 1.00 (calculated by equation 2); this resulted from 412.40 µmol CO_2 $vine^{-1}$ for the WS and 411.02 µmol CO_2 $vine^{-1}$ for the C vine values (calculated by equation 1) (Figure 4).

3.2. Above-ground and below-ground biomass

Irrigation restrictions did not induce any differences in biomass accumulation of perennial above-ground vine organs. Shoots and trunk did not indicate any significant differences in carbon accumulation for any of the sampling dates during the period analysed (Figure 5a and 5b).

The accumulated biomass measurements for the root systems were not significantly different between irrigation treatments (Figure 5c). Considering only new root biomass, a significant ($P<0.05$) increase was observed for the C treatment with respect to the WS treatment throughout the study; with the October 24 exception (Figure 5c). Differences in accumulated biomass in new roots between the C and WS treatments were 63.4, 44.6 and 50.8 % for the September 20, October 4 and November 28 sampling dates, respectively.

The proportion of new root biomass compared total roots biomass was greater in the C treatment compared to the WS treatment and increased as a function of accumulated waster stress (Figure 6). Since leaf fall occurred at the end of October, it was not possible to measure water status on the last measurement date (November 28).

3.3. Starch accumulation

Starch concentrations during the whole period were significantly different between sampling dates for

shoot and trunk organs, in both of the irrigation treatments (Table 1). Significant differences were observed ($P<0.05$) between the treatments on the last measurement date (November 28), when the lowest starch concentrations were registered and ranged from 10.6 and 11.6 %. The highest average starch concentration in C treatment shoots was 16.7 % for the September 20, October 4 and October 24 sampling dates. The C vines had the highest starch concentrations in the trunk on the September 20 and October 4 sampling dates, with an average of 15.7 % (Table 1). The highest starch concentrations in the WS treatment occurred on October 4, in shoots were registered 16.3 % and 15.2 % in the trunk. No significant differences in starch concentration were found in root organs for any sampling date or irrigation treatment, during the experiment.

As observed for dry mass, in all of the perennial organs, the starch content was not significantly different between irrigation treatments for any sampling dates (Figure 7). There were statistical differences between the first (August 25) and the last (November 28) sampling dates within the same irrigation treatments. Shoot starch content did significantly decline from 9.3 g of starch to 7.1 g in the C vines and 6.7 in the WS vines by November 28 (Figure 7a). As with shoots, the minimum starch content in trunk was registered on the last sampling date (November 28), with 8.8 g in both treatments (11.2 g of starch was measured on August 25) (Figure 7b). Over time the starch content in the roots of the C and WS treatments appeared to diverge, but the differences were not statistically significant (Figure 7c).

4. Discussion

One of the most noticeable effects of water stress during post-harvest was the rapid reduction of leaf area through defoliation, with plants accelerating the normal process of leaf senescence apparently to compensate for unfavourable water status conditions (Figure 3). During post-harvest, leaf functioning is considered to play an important role in carbohydrate assimilation until leaf senescence (Loescher et al. 1990, Köse and Ates 2017). In spite of the imposed water stress in our study, the total amount of assimilated carbon per leaf surface area was similar for both treatments throughout the experiment ($\int A_{n\ leaf\ WS} / \int A_{n\ leaf\ C} = 1$) (Figure 4). However, the leaf biomass in WS vines was considerably reduced in comparison with C vines, due to defoliation (Figure 3), which it could have allowed a lower carbohydrate assimilation. The differences between the treatments with A_n were smaller than expected, because the remaining WS leaves demonstrated greater photosynthetic activity than the C vines (Figure 4). In the C vines, the photosynthetic rate was similar to that reported in other studies (Sauvignon blanc, 5 – 11 µmol CO_2 m^{-2} s^{-1}) (Greven et al. 2016). Abiotic factors such as temperature, light

and/or water are known to affect the photosynthetic capacity of vine leaves (Escalona et al. 1999). In the present experiment, however, the main factor responsible for the differences between treatments was the different leaf area (Figure 3). During the stress period, the remaining leaves on the WS vines had a greater A_n, which partially compensated for the impact of the reduction in leaf area attributable to water stress (Figure 4). This compensation may have been the reason why the starch content presented no clear treatment effects (Table 1, Figure 7).

No significant differences were found between the treatments in terms of shoot and trunk dry mass during the course of the experiment (Figure 5a and 5b). The figures 5a and 5b showed a hint of less biomass in the WS vine treatment, but the differences were not statistically significant. At the root level, however, new root formation took place in both treatments, but at different rates (Figure 6). The level of the initial stress imposed on WS on this study may be high enough to restrict the growth rate of new roots and keep this below that of the C treatment, even during periods when the plant water status recovered (Figure 1 and Figure 6). This argument is supported by Figure 6, where is presented a comparison between the water stress integral and the growth of new roots. This was probably related to the reduction in leaf area after the initial stress was applied in WS (Figure 3); this may have limited the photosynthetic capacity of the vine.

Respiration processes necessary for growth and organ maintenance are affected by water stress and, as a consequence, starch content could be also influenced (Flexas et al. 2006, López et al. 2013). Previous studies of vines subjected to water stress conditions have shown differences in starch concentrations and contents (Holzapfel et al. 2010). However, despite the different root growth rates, no significant differences were found in total root biomass (Figure 5c) and the same was true for starch content (Figure 7c). But since the biomass already present in the roots probably was large enough to mask differences, no differences were expected in root biomass and starch content. Although no statistically differences were found on total root dry mass between treatments (Figure 5c), it should not be ignored the apparent differences in root dry mass among vine treatments. Furthermore, no differences between treatments were found in starch concentration (Table 1). The differences that were found were in shoot and trunk starch concentrations corresponding to the last series of measurements taken in the experiment (Table 1). The last measurement date also coincided with the lowest starch content (Figure 7a and 7b) (Greven et al. 2016). In previous studies, starch concentration was evaluated in perennial organs for several grapevine cultivars and locations. Reported trunk starch concentrations ranged from 4 to 14

% (Bates et al. 2002, Zapata et al. 2004, Sadras and Moran 2013), and 10 % for a Chardonnay cultivar in New Zealand (Bennett et al. 2005). The same studies of vine roots reported starch concentrations of 8 to 30 %, and 13 % for Chardonnay (in New Zealand). Our starch concentration values were similar to previous Chardonnay study (14 % in trunk and 12 % in roots, on average) (Table 1). This indicates that the level of water stress applied was not enough to influence the starch concentration in these organs. The differences between the concentrations in the shoots and trunk observed at the end of the experiment may have been related to the conversion of starch into other carbohydrates because no remobilization appeared to take place at the root level (starch values remaining constant, Table 1). The decrease on starch concentration in shoots and trunk after leaf fall (November 28, Table 1) could have been associated with the demand for carbohydrates for new root growth, maintaining organ respiration, or acclimatization of the grapevines to low temperatures. This is because increasing vine hardiness to winter conditions requires the conversion of starch into soluble sugars when temperatures fall below 5 ºC and the days become shorter in the middle of winter (Hamman et al. 1996, Keller 2010, Zufferey et al. 2012). These environmental conditions were similar to those corresponding to the last sampling measurements taken in the study (Figure 2).

Maintaining starch concentrations and root biomass in the WS treatment responded to a redistribution of carbohydrate assimilates on shoot and trunk reserves organs. Also, it responds to a conservative strategy for preserving carbohydrates in the form of starch to ensure carbon reserves for subsequent spring growth. Water stress is known to affect root growth in vines (Eapen et al. 2005, Comas et al. 2010, Maihemuti et al. 2016). The reduction in root growth induced by the water stress added to the lack of fruits in the post-harvest period reduced the potentially available sinks and favoured the allocation of new photosynthates towards reserves (Iniesta et al. 2009). Furthermore, pre-harvest reserve replenishment has been reported to begin during fruit maturation, when berry sugar accumulation slows; this means that reserve accumulation in roots could have started before and they may be replenished enough by harvest (Candolfi-Vasconcelos et al. 1994, Holzapfel et al. 2006, Rossouw et al. 2017). If this is so, even though the WS vines were stressed, they may have still been able to keep similar concentrations of reserves as the well-watered plants and this would have allowed them to regrow in the next season. This would imply that vines either have a conservation strategy that allows them to maintain carbohydrates in the form of starch, which gives priority to the survival of permanent structures over any increase in vine size (Greven et al. 2016). According to Greven et al. (2016), the carbohydrate dynamics

related to storage in reserve organs suggests that the trunk may serve as a relevant, albeit transitional, reserve storage organ between the root system and the rest of the vine, and as the most accessible storage sink. Roots, on the other hand, are widely considered to be the most important storage reserve organs in vines (Scholefield et al. 1978, Loescher et al. 1990, Bates et al. 2002).

Containers do not adequately recreate and represent field conditions (Bravdo 2005), because they prevent roots from spreading as widely as they would in soil conditions (Zapata et al. 2001). Furthermore, different stomatal closure processes could be involved with vines grown in soil, such as abscisic acid signalling (Vandeleur et al. 2009). This experiment may point out that water stress during post-harvest "forces" allocation of assimilates towards reserves, thereby allowing plants to maintain their reserves for the following season.

The early defoliation of vines, after several consecutive years under warm conditions and water limitations, has been reported to influence carbohydrate reserves. As a result in the subsequent seasons, it occurred the reductions in yields and poorer vegetative growth, because new growth is dependent on pre-existing reserves (Vaillant-Gaveau et al. 2014, Greven et al. 2016, Köse and Ates 2017). Under the conditions where our study was developed, we did not evaluate variations on carbohydrate reserves in front of water limitation. But it could be hypothesised that an accumulative effect on vine reserves during post-harvest period under these conditions may deplete them. As it has showed on this work, the most significant effect evaluated due to water stress was the reduction of fine root growth, which it may hinder the vegetative growth on the following season. Recent research related to climate change within the same study area has reported reductions in annual precipitation, in both autumn and winter, and an increase in temperatures, especially during summer (Gonçalves et al. 2014). Which it coincided according with the environmental conditions in which the work was tried to be carried out. Moreover, phenological shifts associated with increasing temperatures have been reported in several wine-growing regions (Jones and Davis 2000, Duchêne et al. 2010, Petrie and Sadras 2008). One of the main possible consequences of this shifts may be the enlargement of the post-harvest, its occurrence into warmer conditions and the increase of the irrigation water requirements (Hall et al. 2016). It is substantial to consider the possible interactions in grapevine behaviour, taking into consideration changes in environmental conditions, shifts in phenological events and carbon balances and partitioning (Ollat and Touzard 2014).

5. Conclusions

The main effect of water stress on grapevines during the post-harvest period was the defoliation of the vines and reduction in their total leaf area. Supplying full water demands until leaf fall permitted the maintenance of photosynthetic leaf area and consequently a higher level of carbohydrate accumulation, along with the formation of new roots which are responsible for high water and nutrient uptake. The lack of water caused vines to respond with variations on biomass accumulation between above and below ground perennial organs, indicating a high response in carbon economy in order to favour the survival of the permanent structures rather than total increases in vine size. Moreover, water stress did not influence the main storage organ, the roots, keeping the biomass and starch concentrations.

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Table 1. Starch concentrations of shoots and trunk (perennial above-ground organs) and roots (below-ground reserve organ) for vines harvested during the course of the post-harvest treatments.

Sampling date (month/day)	Treatment					
	Control (%)			Water Stress (%)		
	Shoots	*Trunk*	*Tick roots*	*Shoots*	*Trunk*	*Tick roots*
Starting date 08/25	14.2 ± 0.5^{b}	13.5 ± 0.3^{b}	12.3 ± 1.2^{a}	14.2 ± 0.5^{b}	13.5 ± 0.3^{b}	12.3 ± 1.2^{a}
09/20	16.7 ± 0.2^{a}	15.7 ± 0.2^{a}	12.5 ± 0.8^{a}	15.1 ± 0.5^{ab}	14.9 ± 0.4^{ab}	13.0 ± 1.6^{a}
10/04	16.6 ± 0.2^{a}	15.8 ± 0.2^{a}	14.0 ± 1.0^{a}	16.3 ± 0.2^{a}	15.2 ± 0.2^{a}	12.2 ± 0.4^{a}
10/24	16.8 ± 0.5^{a}	15.0 ± 0.2^{ab}	11.3 ± 0.7^{a}	15.7 ± 0.5^{ab}	14.8 ± 0.4^{ab}	12.5 ± 0.5^{a}
11/28	11.6 ± 0.3^{c}	10.7 ± 0.3^{c}	13.3 ± 1.1^{a}	10.9 ± 0.3^{c}	10.6 ± 0.4^{c}	11.3 ± 0.7^{a}

Different letters mean significant differences on starch concentration between sampling dates in the same organ and in the same irrigation treatment ($P<0.05$).

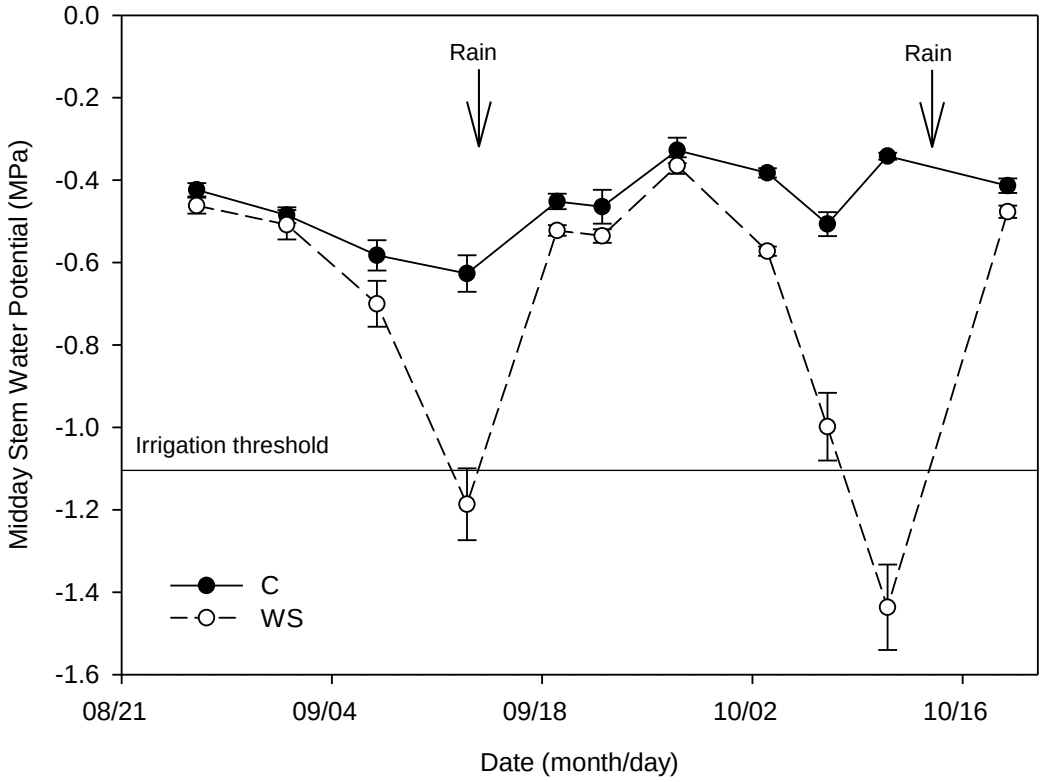

Figure 1. Post-harvest period patterns of midday stem water potential for vines under control (C) and water stress (WS) treatments. Natural leaf fall occurred on October 19. The irrigation threshold in the WS treatment was defined as -1.1 MPa. The bars indicate the standard error of the mean.

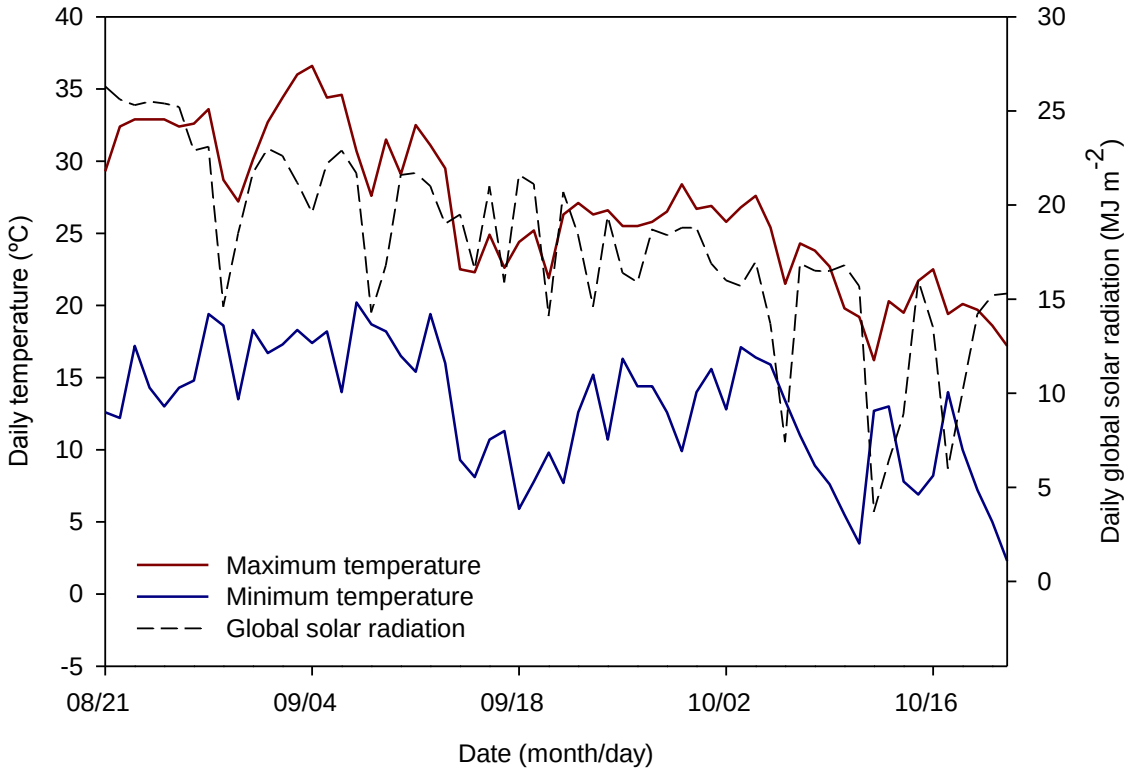

Figure 2. Climate summary during the experimental period with daily maximum and minimum temperature and daily global solar radiation. Environmental data was retrieved from the nearest weather station (1 km) from the study location (Raïmat, www.ruralcat.net/web/guest/agrometeo.estacions).

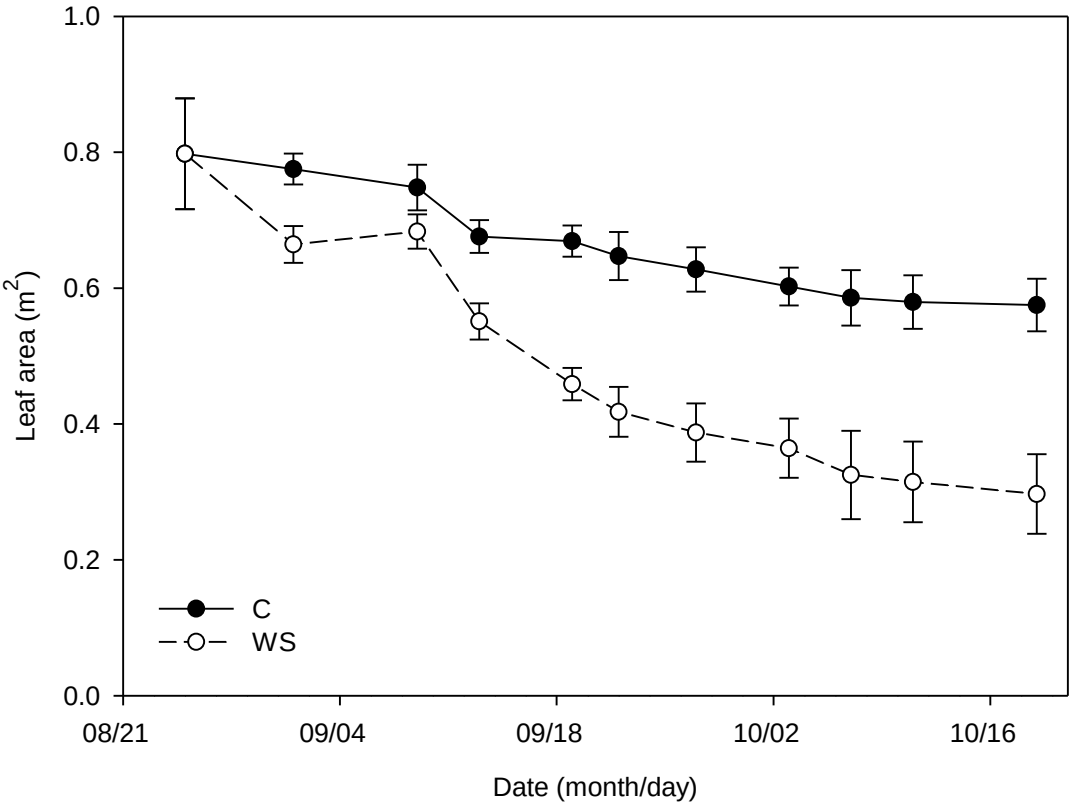

Figure 3. Leaf area pattern until leaf fall on vines under control (C) and water stress (WS) treatments. Natural leaf fall occurred on October 19.The values represent the means for five vines per treatment and the bars indicate the standard error of the mean.

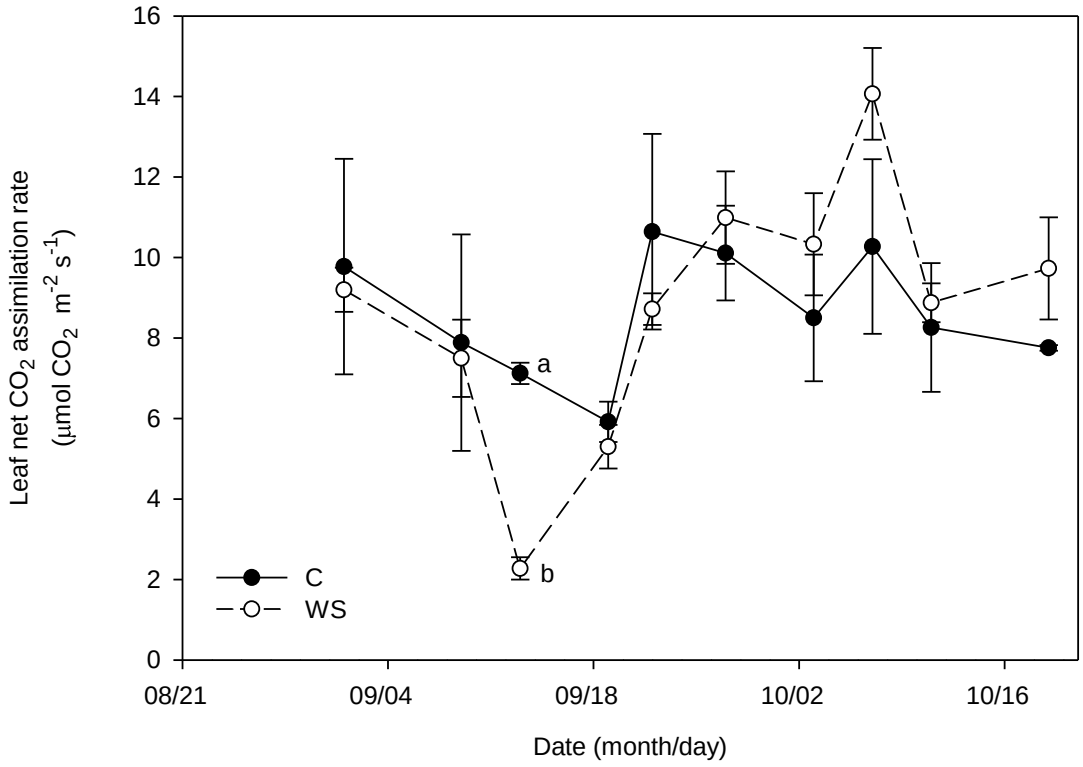

Figure 4. Post-harvest period patterns of leaf net CO_2 assimilation rate for vines under control (C) and water stress (WS) treatments. Natural leaf fall occurred on October 19. Bars indicate the standard error of the mean. Different letters indicate significant differences between irrigation treatments for the same date ($P<0.05$).

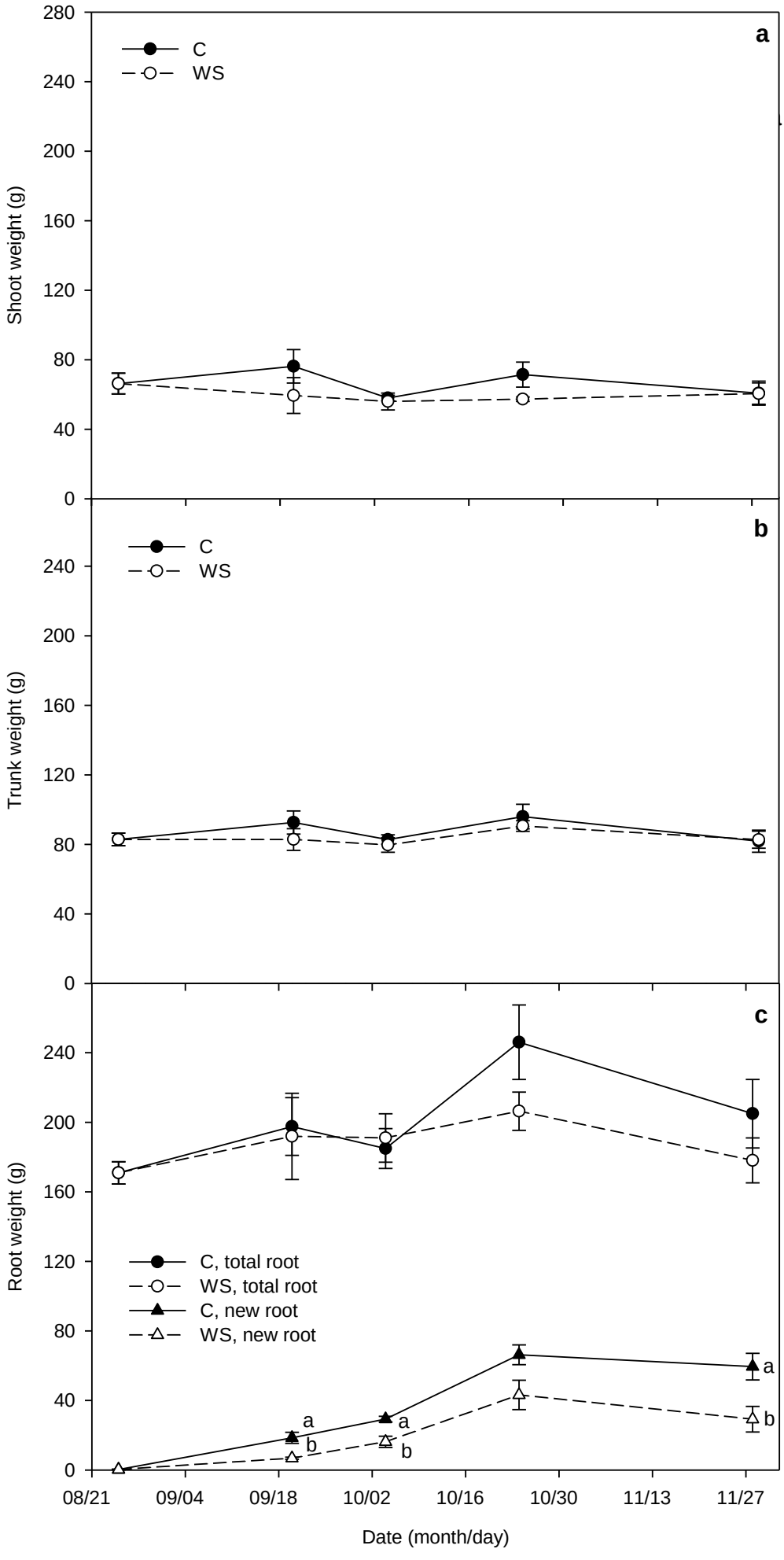
a
C
WS
Shoot weight (g)
280
240
200
160
120
80
40
0
b
C
WS
Trunk weight (g)
240
200
160
120
80
40
0
c
C, total root
WS, total root
C, new root
WS, new root
Root weight (g)
240
200
160
120
80
40
0
a
a
b
b
a
b
08/21
09/04
09/18
10/02
10/16
10/30
11/13
11/27
Date (month/day)

Figure 5. Post-harvest period patterns for dry mass in shoot (a), trunk (b), total root and new root organs (c) under control (C) and water stress (WS) treatments. The values represent the means of five vines per treatment and the bars indicate the standard error of the mean. There were no significant differences between irrigation treatments for the same sampling date ($P<0.05$).

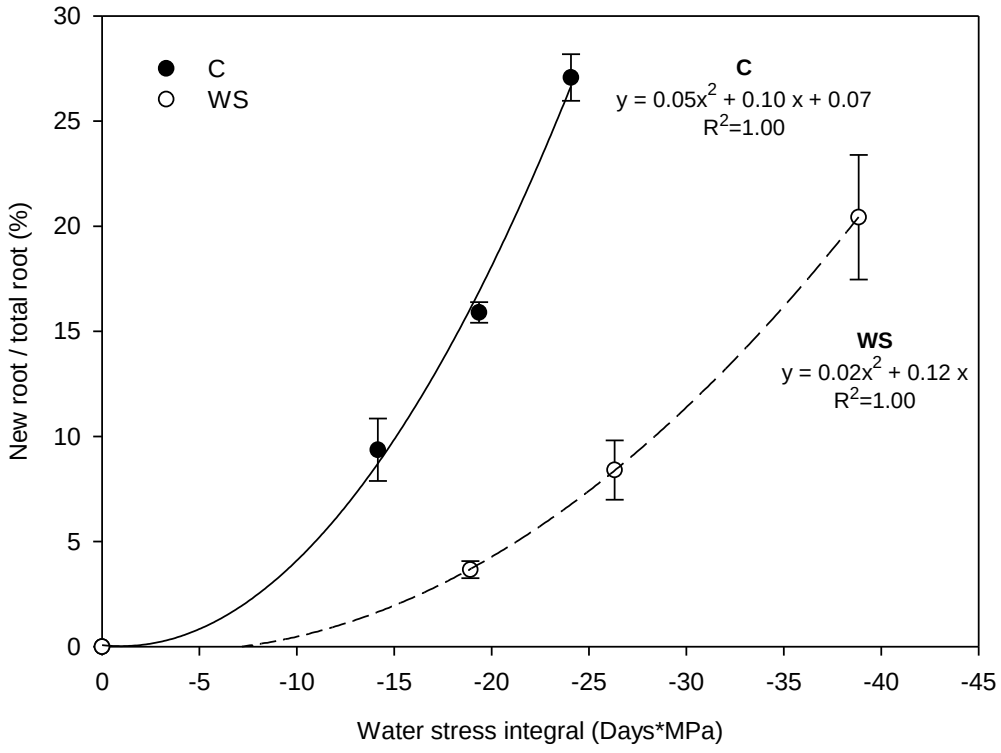

Figure 6. Proportion of new root to total root weight in response to the cumulative water stress integral of vines under the control (C) and water stress (WS) treatments. The values represent means for five vines per treatment on the August 25, September 20, October 4 and October 24 sampling dates. Bars indicate the standard error of the mean. Equations represent the polynomial adjustment of the measures.

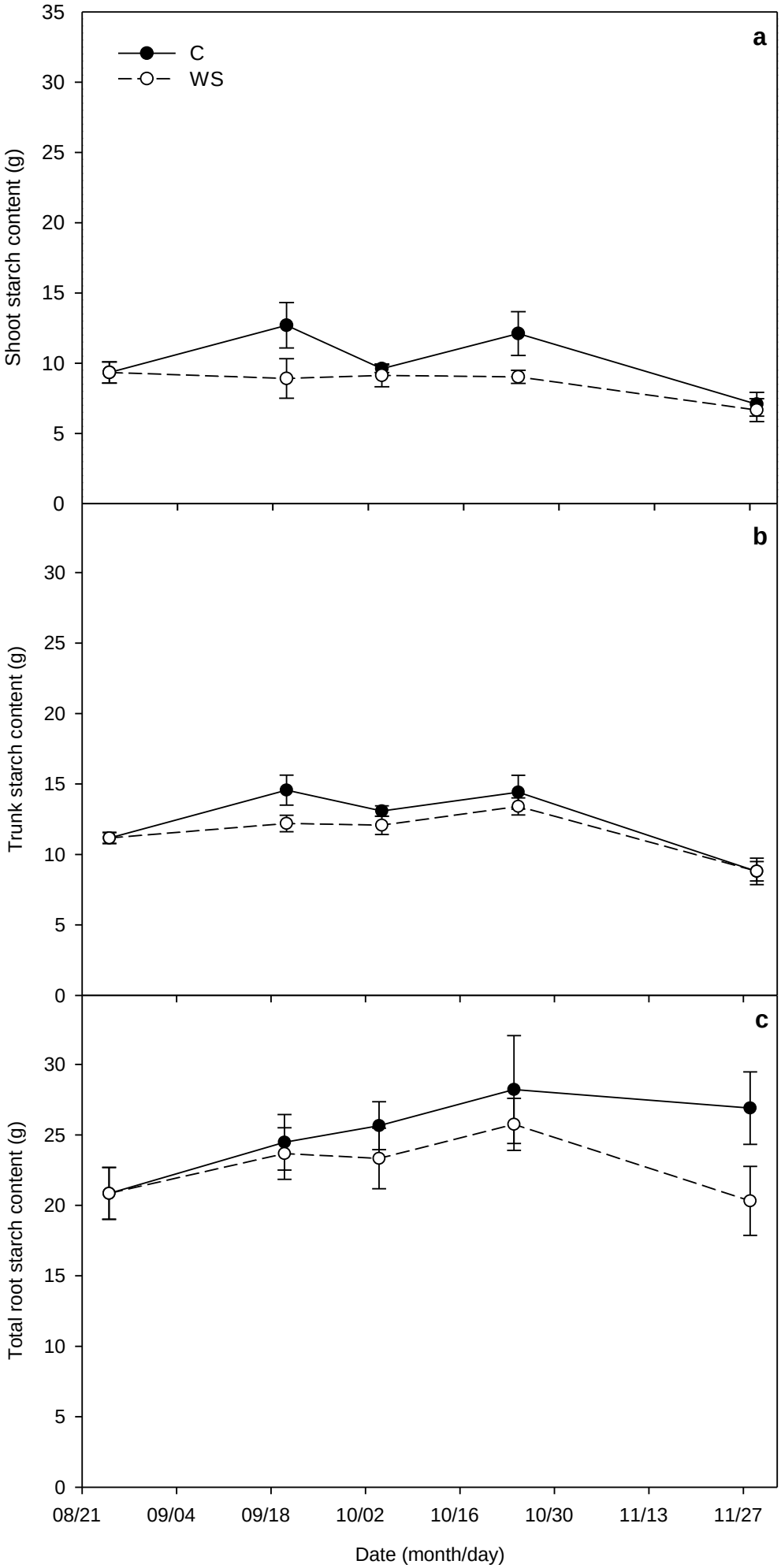
a
C
WS
Shoot starch content (g)
35
30
25
20
15
10
5
0
b
Trunk starch content (g)
30
25
20
15
10
5
0
c
Total root starch content (g)
30
25
20
15
10
5
0
08/21
09/04
09/18
10/02
10/16
10/30
11/13
11/27
Date (month/day)

Figure 7. Post-harvest patterns of starch content in shoot (a), trunk (b) and total root (c) organs under control (C) and water stress (WS) treatments. The values represent the means for five vines per treatment and the bars indicate the standard error. There were no significant differences between irrigation treatments for the same sampling date ($P<0.05$).