Research paper

Fruit load governs transpiration of olive trees

Amnon Bustan[1,2], Arnon Dag[1], Uri Yermiyahu[1], Ran Erel[1], Eugene Presnov[1], Nurit Agam[3], Dilia Kool[1],
Joost Iwema[1,4,5], Isaac Zipori[1] and Alon Ben-Gal[1,6]

[1]Gilat Research Center, Agricultural Research Organization, mobile post Negev 85280, Israel; [2]Desert Agro-Research Center, Ramat-Negev R&D, D.N. Halutza 85515, Israel;
[3]Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Be'er Sheva 84990, Israel; [4]Soil Physics, Ecohydrology and Groundwater Management,
Wageningen University, 6700AA Wageningen, The Netherlands; [5]Present address: Department of Civil Engineering, University of Bristol, Bristol BS8 1TR, UK; [6]Corresponding
author (bengal@volcani.agri.gov.il)

We tested the hypothesis that whole-tree water consumption of olives (*Olea europaea* L.) is fruit load-dependent and investigated the driving physiological mechanisms. Fruit load was manipulated in mature olives grown in weighing-drainage lysimeters. Fruit was thinned or entirely removed from trees at three separate stages of growth: early, mid and late in the season. Tree-scale transpiration, calculated from lysimeter water balance, was found to be a function of fruit load, canopy size and weather conditions. Fruit removal caused an immediate decline in water consumption, measured as whole-plant transpiration normalized to tree size, which persisted until the end of the season. The later the execution of fruit removal, the greater was the response. The amount of water transpired by a fruit-loaded tree was found to be roughly 30% greater than that of an equivalent low- or nonyielding tree. The tree-scale response to fruit was reflected in stem water potential but was not mirrored in leaf-scale physiological measurements of stomatal conductance or photosynthesis. Trees with low or no fruit load had higher vegetative growth rates. However, no significant difference was observed in the overall aboveground dry biomass among groups, when fruit was included. This case, where carbon sources and sinks were both not limiting, suggests that the role of fruit on water consumption involves signaling and alterations in hydraulic properties of vascular tissues and tree organs.

Keywords: *Olea europaea*, photosynthesis, stomatal regulation, vegetative growth, water potential, yield.

Introduction

It is largely accepted and understood that the presence of fruit on plants influences source–sink carbon relationships and actively or passively affects water status and water consumption (Naor 2014, Sade and Moshelion 2014). That said, quantification of how water consumption or water requirements are altered by fruit presence or fruit load has rarely been addressed (Guichard et al. 2005). Olive (*Olea europaea* L.) production has historical importance throughout the Mediterranean, where olive oil is a fundamental component of the regional diet (Serra-Majem et al. 2003). Traditionally, olives are not irrigated; however, in recent decades, water application has become recognized as being constructive and effective (Lavee 2011). Under typical Mediterranean climatic conditions (hot and dry summers),

irrigation can enhance olive fruit and oil yields by as much as fourfold (Lavee et al. 1990, Moriana et al. 2003, Grattan et al. 2006).

Water is a limited resource in much of the Mediterranean basin as well as in newer regions of olive cultivation. Therefore, substantial efforts are made to optimize fruit and oil production by manipulating quantity and regime of irrigation water supply (Iniesta et al. 2009). However, understanding of olive tree water status and strategies for orchard water management typically ignore key intrinsic processes related to fruit development and oil accumulation that possibly lead to fruit load effects on water requirements. The olive is well adapted to the Mediterranean climate (Connor 2005), where seasonal phenological–physiological requirements for photosynthates and for water

coincide with typical prevalent summertime drought-related environmental stresses. Having also a strong tendency for biannual bearing (Lavee 2006), the olive represents a particularly interesting case for the study of interactions between fruit load and water status and consumption interactions.

The seasonal reproductive process in fruit trees becomes the plant's dominant carbon sink, particularly in modern heavily yielding orchards. Carbon demand has been found to spike during bloom (Bustan and Goldschmidt 1998), and when an ample number of fruit is set almost simultaneously, carbon source limitation can cause significant fruit drop (Zucconi et al. 1978, Rapoport and Rallo 1991, Rivas et al. 2006). After retardation of fruit abscission mechanisms (Huberman et al. 1983, Castillo-Llanque and Rapoport 2009) and the final establishment of the ultimate number of fruit on a tree, the fruit that first rapidly grow and, in olives, consequentially accumulate substantial amounts of oil present an increasing demand for carbohydrates (Bustan et al. 2011). These carbon demands can be met by enhanced utilization of stored carbohydrate reserves. In deciduous fruit trees, the early stages of reproductive growth and development rely on the remobilization of stored carbon (Körner 2003). In alternate bearing citrus cultivars, the concentration of nonstructural carbohydrates may undergo extreme fluctuations due to differences in fruit load between years (Goldschmidt and Golomb 1982). In olive, in spite of a significant tendency to alternate bearing, the role of stored carbohydrates supporting the developing crop is less pronounced (Bustan et al. 2011).

An expansion of the foliage area, essentially increasing photoassimilation capacity, can theoretically assist to bridge the carbon gap brought on by a heavy fruit load. However, concurrent vegetative growth is substantially inhibited by the developing fruit in many species of fruit trees. Particularly in olives, vegetative and reproductive growth seldom occur simultaneously (Lavee 2006, Dag et al. 2010). Thus, coping with the carbon challenge apparently involves a significant increase in daily primary production by either raising the carbon exchange rate (CER) or by expanding time of stomatal opening and gas exchange processes. Carbon source limitation has been suggested as the prevalent situation (Muller et al. 2011), in which CER is consistently maintained at the maximum level allowed by environmental factors such as solar irradiation, temperature and humidity. Alternatively, assuming that sink limitations control carbon assimilation, CER would be up-regulated when sink demands increase and down-regulated when the demands decline. While most of the studies addressing fruit load effects on photosynthesis showed significant reduction in CER following fruit removal (Avery 1975, DeJong 1986, Berman and DeJong 1996, Naor et al. 1997, Syvertsen et al. 2003, Wünsche and Ferguson 2005, Haouari et al. 2013, Silber et al. 2013a), up-regulation of CER by rising sink demands is difficult to prove. It may be postulated that, as long as sufficient sink demands are maintained in a tree, carbon supply would be limited by the current source capacity. However, declining sink demands might limit CER through feedback inhibition mechanisms (Gifford and Evans 1981). While some authors have attributed CER decline to metabolic feedback inhibition by carbohydrate species accumulating in the source leaf (Goldschmidt and Huber 1992, Syvertsen et al. 2003, Silber et al. 2013a), others have pointed to direct or indirect effects on stomatal conductance (g_s) (DeJong 1986, Naor et al. 1997, Martín-Vertedor et al. 2011a, Silber et al. 2013b). If stomatal regulation is involved, reduced water consumption may be a natural consequence of decreasing g_s (Martín-Vertedor et al. 2011b). The question of whether trees are also capable (and by what means) of an opposite course, enhancing CER and water uptake in response to the intensity of their reproductive phase, remains open.

Crop water requirements are typically determined according to the '$K_C ET_O$' approach (Allen et al. 1998), relying on standard meteorological data and crop coefficients. The plant is conceptually addressed as a system passively responding to the combined effects of soil water availability and the atmospheric demand. Fruit load is known to significantly affect water status in many fruit tree species (Naor 2006, Intrigliolo and Castel 2007, Conejero et al. 2010, Silber et al. 2013b) but is not considered a factor in evaluating crop water requirements. Since negligible amounts of water are transpired or taken up by fruit compared with leaves, indirect explanations of fruit effects on water status and possible influences on water requirements are, therefore, necessary. One explanation is the ability of a species to move along an isohydric/anisohydric scale (Klein 2014), either in terms of the above-mentioned consequences of increasing demands for carbohydrates or associated with mechanisms augmenting water availability to developing organs. Sade and Moshelion (2014) postulated that the presence of fruit might shift plants from isohydric to anisohydric stomatal behavior.

The majority of the experimental work to determine tree water requirements has been carried out under field conditions, where plant water uptake cannot be measured directly. In field experiments, indirect parameters such as stem or trunk diameter variations, stem water potential (STWP), g_s or sap flow are used as indicators of water consumption. In light of the complexity and difficulty of translating data from such parameters into quantified water consumption, a direct holistic approach would seem more appropriate. In spite of inherent differences from field-grown trees due to innate boundary conditions, lysimeter-grown trees provide a unique opportunity to directly, accurately and reliably complete the water balance and directly measure plant water consumption during successive growth stages along seasons and years (Ben-Gal et al. 2010, Agam et al. 2013, Silber et al. 2013a). We hypothesized that quantitative whole-tree water consumption of olives is fruit load dependent. The objectives of the study were to test this hypothesis by (i) directly and continuously determining the effects of fruit load on olive tree water

consumption and (ii) investigating the driving physiological mechanisms causing these effects.

Materials and methods

Lysimeters and water balance

Single 4-year-old 'Barnea' olive trees were grown in fifteen 2.5 m³ volume free-standing lysimeters at the Gilat Research Center in the northwestern Negev, Israel (31°20′N, 34°40′E) (Ben-Gal et al. 2010). Each lysimeter consisted of a polyethylene container (1.4 m high × 1.5 m diameter) filled with loamy sand soil, a bottom layer of highly conductive porous rockwool media in contact with the soil and drainage piping filled with the rockwool extending downward from the lysimeter bottom. The rockwool drainage extension (Ben-Gal and Shani 2002) disallowed saturation at the lower soil boundary while permitting water to move out of the soil and be collected. The trees in lysimeters were automatically provided water and fertilizer and drainage water was automatically collected (Tripler et al. 2012). Each lysimeter's soil surface was covered by a water permeable geotextile (Non-Woven Geotextile, 500 g m⁻², Noam-Urim, Negev, Israel) to minimize evaporation losses. The lysimeters were placed every 2.5 m, four to a row in four rows with 4 m spacing and were surrounded by border trees. The second lysimeter in the second row was treeless. Each individual lysimeter was positioned on a square weighing platform with load cells situated in each corner. By distributing load cell output current only over the relevant range of interest (4–5 tons), a resulting resolution of ±15.5 g was reached. Evapotranspiration (ET) was calculated daily according to: $ET = I - D - \Delta W$, where I is irrigation (pre-determined), D is drainage (measured) and ΔW is change in soil water (derived from the change in lysimeter mass). There was no rainfall during the experimental period. The trees were irrigated daily, with quantities exceeding (by ~20%) the previous day's transpiration rates as calculated from the weight data of the lysimeters. In order to evaluate whether fruit load would particularly affect plant water status during times of water stress, all the trees were subjected to short-term controlled moderate drought three times during the experimental period. Drought was induced by reducing irrigation to half of the previous day's measured ET. Drought periods were DOY 164–167 (13–15 June), DOY 207–209 (26–28 July) and DOY 262–264 (19–21 September). Nutrients were added to the irrigation solution as liquid commercial 7 : 3 : 7 (N : P_2O_5 : K_2O) fertilizer (Fertilizers and Chemicals LTD, Haifa, Israel) at a continuous concentration in irrigation solution of 50 p.p.m. nitrogen.

Manipulations of fruit load

All trees received identical treatment from planting in June 2008 until the beginning of the current experiment (Spring 2011). At bloom, trees were randomly designated to five groups replicated three times: control; early (23 May, DOY 141, just after fruit set)

fruit removal; early fruit thinning (also on 23 May, DOY 141, every second fruit); mid-season (7 July, DOY 186) fruit removal, during pit hardening; and late-season (7 September, DOY 248) fruit removal, during oil accumulation. Fruit thinning and removal were carried out manually and the fruit were weighed and counted for each tree. Final fruit harvest of control and thinned trees took place on 31 October, DOY 304. Subsequent to removal of all fruit, when the actual load of each tree became clear, the trees were retroactively regrouped according to status of fruit load. A summary of fruit load per tree throughout the experiment is given in Table 1. Trees initially carrying >10,000 fruits (12 trees) were considered high-yielders (HY), while trees with initially <10,000 fruits (3 trees) were termed as originally low-yielders (OLY). In each event of fruit load manipulation, trees were discarded from the HY group and designated to the early-season (DOY 141), mid-season (DOY 186) or late-season (DOY 248) fruit removal groups (EFR, MFR and LFR groups, respectively). Some manipulated trees remained fruitless within the OLY group, or remained within the HY group, as fruit thinning was insufficient to send them below the threshold of 10,000 fruits per tree. Thus, the HY group decreased gradually from 12 to 4 trees at harvest, while the OLY, EFR, MFR and LFR groups consisted of 3, 3, 2 and 3 trees, respectively (Table 1).

In further analyses of the results, trees were designated to only two groups, HY and LY, according to their current fruit load status (above and below 10,000 fruit per tree) at each of the four phases of the experiment along the season: I (DOY 100–140), II

Table 1. Actual number of fruit per tree during the four experimental periods (I, DOY 100–140; II, DOY 141–185; III, DOY 186–250; and IV, DOY 251–304), as determined by the fruit thinning/removal treatments. Control HY—fruit number exceeded 10,000 per tree throughout the season, whether thinned or not; OLY—fruit number <10,000 per tree throughout the season, whether thinned or not; EFR, MFR and LFR—early, mid and late season fruit removal, respectively, that shifted trees from high-yield (HY) to low-yield/no fruit (LY) status. Clear and shaded cells indicate HY and LY trees, respectively.

Tree #	Treatment	Experimental period			
		I	II	III	IV
2	Control HY	17,793	17,793	17,793	17,793
5	Control HY	36,301	20,133	20,133	20,133
8	Control HY	18,794	18,794	18,794	18,794
15	Control HY	26,851	16,842	16,842	16,842
9	OLY	3433	0	0	0
10	OLY	5610	5610	5610	5610
14	OLY	5744	5744	0	0
4	EFR	13,338	6744	6744	6744
6	EFR	53,796	0	0	0
13	EFR	29,625	0	0	0
3	MFR	28,260	28,260	0	0
12	MFR	45,718	45,718	0	0
1	LFR	21,365	21,365	21,365	0
7	LFR	25,692	25,692	25,692	0
11	LFR	25,620	25,620	25,620	0

(DOY 141–185), III (DOY 186–247) and IV (DOY 248–304). Consequently, while the HY group decreased accordingly from 12 to 4 trees as described, the number of trees of the LY group gradually increased from 3 to 11 at the end of the experiment (Table 1).

Vegetative growth

Trunk cross-sectional area (TCSA) was calculated using periodical measurement of trunk circumference. Circumference was measured at a marked point on the trunk ~50 cm above the soil. At the end of the experiment, after final harvest of fruit, trees were removed from the lysimeters, separated into leaves, branches, limbs and trunk, dried at 70 °C and weighed. Aboveground biomass was measured and leaf area was calculated using a portable leaf area meter (LI-3000, LI-COR, Lincoln, NE, USA).

Physiology and water status

Measurements were conducted on stems and leaves 0.5–1.5 m above the soil surface. Midday STWP was measured weekly around solar noon, as described by Shackel et al. (1997), on single shoot terminal sections with six to seven leaves covered at least 2 h in advance by sealed aluminum plastic bags. Shoot sections were taken from the northern (shaded) side of the trees' canopies. Gas exchange, g_s and fluorescence-based measurements were taken every 2–3 weeks around solar noon, on young but fully grown leaves between 5 and 20 cm from the shoot tip. For each tree, five replicate leaves, uniformly distributed over sun-exposed canopy, were measured. Carbon exchange, g_s and electron transport rate (ETR) were measured with a portable gas exchange system (LI-6400, LI-COR). The chamber was set to mimic outside conditions. The midday physiological measurements were conducted between 12:30 and 13:30 h. On 4 August 2011, diurnal (predawn till sunset) patterns were evaluated as each of the physiological parameters was measured once an hour.

Data analysis

Relationships between leaf area and biomass to TCSA and of water consumption to number of fruits per tree were tested using SigmaPlot (Systat Software, San Jose, CA, USA). Linear regression lines were fitted to data. Effect of treatments on measurements of STWP and leaf-scale carbon exchange, conductance and ETR was analyzed by one-way analysis of variance (Tukey–Kramer multiple comparisons test) using JMP statistical software (SAS Institute, Cary, NC, USA).

Results

Effect of fruit load on tree specific water consumption

Comparative analysis of net water consumption of each individual tree confirmed substantial variability among trees having similar fruit load, attributed to significant differences in canopy size (leaf area). Evaluation of results and effects of treatments therefore required methods for normalization of the data. The aboveground dry biomass of each tree was determined a month after final fruit harvest (Table 2). Trunk cross-sectional area was calculated from the periodical measurement of trunk circumference throughout the reproductive season. A strong linear correlation was found between final TCSA and both the final aboveground dry biomass and the calculated total leaf area (Figure 1). Thus, the recurrent TCSA measured on individual trees along the season was employed as a tree-size normalizing factor for water consumption, giving rise to the parameter of specific water consumption (SPWC), quantified as liters per TCSA (cm^2) per tree per day.

Figure 2 shows the average daily SPWC of individual trees during each of four experimental periods of the season. The basal SPWC, given by trees with no or low fruit loads increased with time, was indicated by the movement of the interception point upward from <0.4 at the beginning of the season to ~0.63 l cm^{-2} day^{-1} at its end. Between bloom and final fruit

Table 2. Final dry matter distribution among aboveground tree organs. Different letters indicate significant differences within columns at $P < 0.05$.

| Treatment	Vegetative organs					Fruit[1]	Total
	Trunk	Limbs	Branches	Leaves	Total		
Dry biomass (kg tree^{-1})							
High-yield control	13.2a	50.4a	31.4	12.1	107.1a	24.4c	131.4
Low-yield control	13.8ab	62.1b	31.1	13.0	119.9ab	3.8a	123.7
Early fruit removal	14.3b	62.3b	33.4	14.2	124.2b	6.3a	130.5
Mid fruit removal	15.8b	64.1b	33.8	14.1	127.7b	15.3ab	143.0
Late fruit removal	12.9a	47.0a	32.5	14.3	106.8a	19.8b	126.6
Dry biomass (%)							
High-yield control	10.1	38.3a	23.8	9.2a	81.3a	18.7c	100
Low-yield control	11.3	49.8b	25.5	10.7ab	97.3c	2.7a	100
Early fruit removal	11.1	46.7b	25.7	10.8b	94.4bc	5.6a	100
Mid fruit removal	11.1	45.0b	23.5	9.7ab	89.4b	10.6b	100
Late fruit removal	10.2	36.7a	25.7	11.3b	83.9a	16.1c	100

[1]At fruit removal date or harvest.
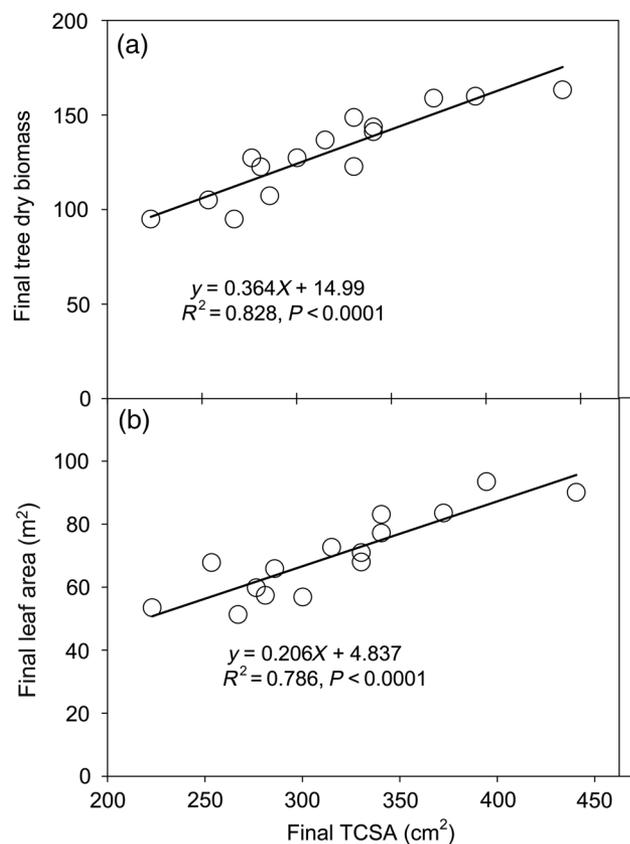
Figure 1. Relationship between TCSA, tree biomass (a) and leaf area (b) at time of tree removal after final fruit harvest in November 2011.
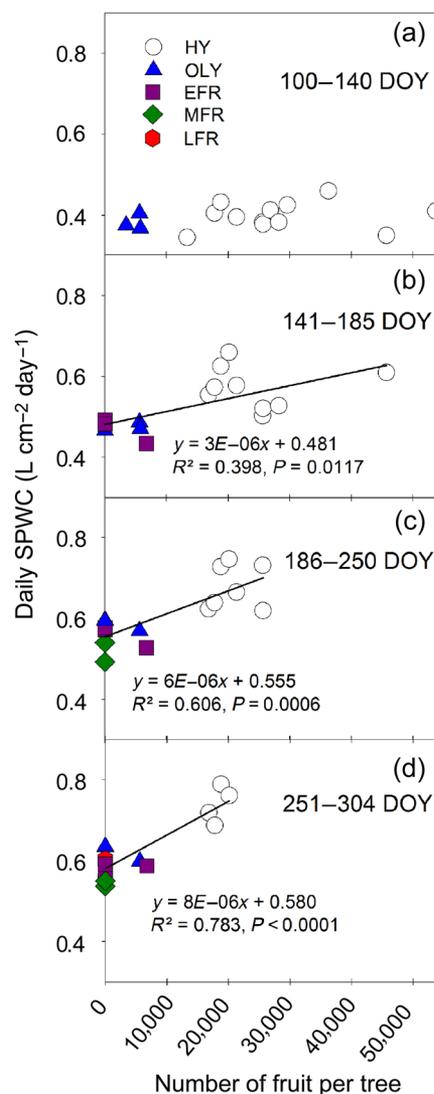

Figure 2. Periodical daily average of calculated SPWC for lysimeter-grown olive trees as a function of current fruit load at four subsequent phenological periods from bloom to final harvest. Filled symbols present individual trees with current fruit load <10,000 fruit, as follows: originally low-yielding (OLY), early (DOY 141) thinned or defruited (EFR), mid-season (DOY 185, MFR) and late-season (DOY 248, LFR) defruited trees. Empty symbols represent trees with current fruit load >10,000 (HY).

set (DOY 100–140), SPWC was irresponsive to fruit load. During the second period (until DOY 185), the weak increase of SPWC was hardly significant. From that point on, however, two distinct groups of trees were clearly distinguished by differing SPWC: high-yielding trees had characteristically high SPWC, while low-yielding and defruited trees had lower SPWC values. Once defruited, trees moved from the higher to the lower SPWC group. The influence of fruit load on SPWC increased gradually along the season, as indicated by the significantly steeper slope of the correlation curve during periods III and IV (DOY 186–250 and 251–304 respectively) (Figure 2).

Figure 3a presents full-season patterns of SPWC of the five groups of trees, sorted according to manipulations of their fruit yield. The HY trees with >10,000 fruit per tree consistently displayed the highest SPWC. The OLY trees, with <10,000 fruit from the beginning, had significantly lower SPWC values quite early in the season and remained relatively low until the end. Early removal of fruit just after final fruit set differentiated this group from the HY and sent it to the lowest SPWC level. The SPWC of EFR dropped by ~15–20% below its original HY group, and remained 5% below that of OLY trees (Figure 3b). The effect of the mid-season fruit removal was more significant, causing an immediate drop of SPWC, again splitting the MFR

trees from HY and causing them to replace the EFR trees as the group with the lowest SPWC. Within a week after fruit removal, the SPWC of the MFR trees dropped to 25% below HY. Their SPWC then fluctuated within a range of 25–40% below the HY trees and 10–25% below the OLY trees until harvest. The latest fruit removal also reduced SPWC rapidly and significantly below those of the HY and OLY groups. After harvest, SPWC of the high-yielding trees dropped steeply to converge with those of the other trees. Thus, extensive fruit thinning or defruiting was always associated with an immediate substantial decline in tree water consumption and its stabilization at a new, significantly lower level thereafter.
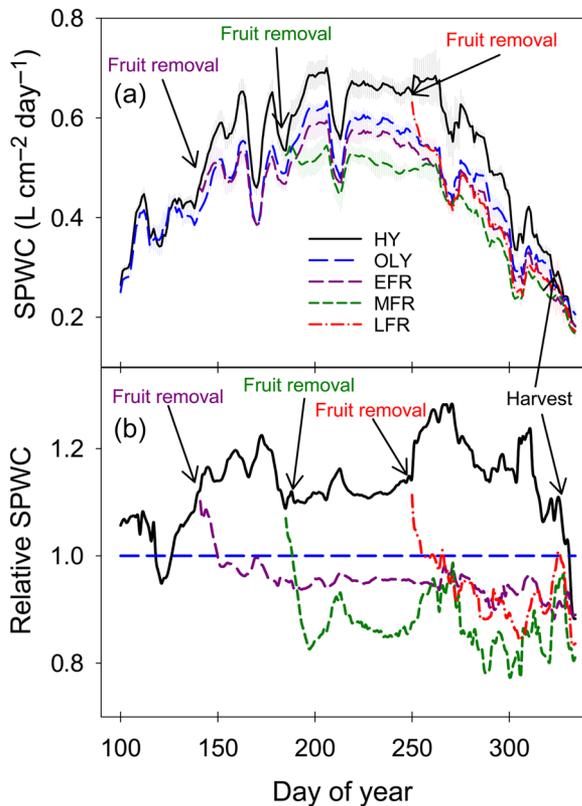
Figure 3. Time course of SPWC for olive fruit season in 2011 (a). Specific water consumption calculated as tree-scale daily ET (l)/TCSA (cm^2). Lysimeter-grown olive trees divided into treatment classes: HY (high yielding) >10,000 fruits per tree, OLY (originally low yielding) <10,000 fruits/tree, EFR (early fruit removal), MFR (mid fruit removal) and LFR (late fruit removal). Relative SPWC (b)—SPWC normalized to the OLY group. Error bars are standard errors.
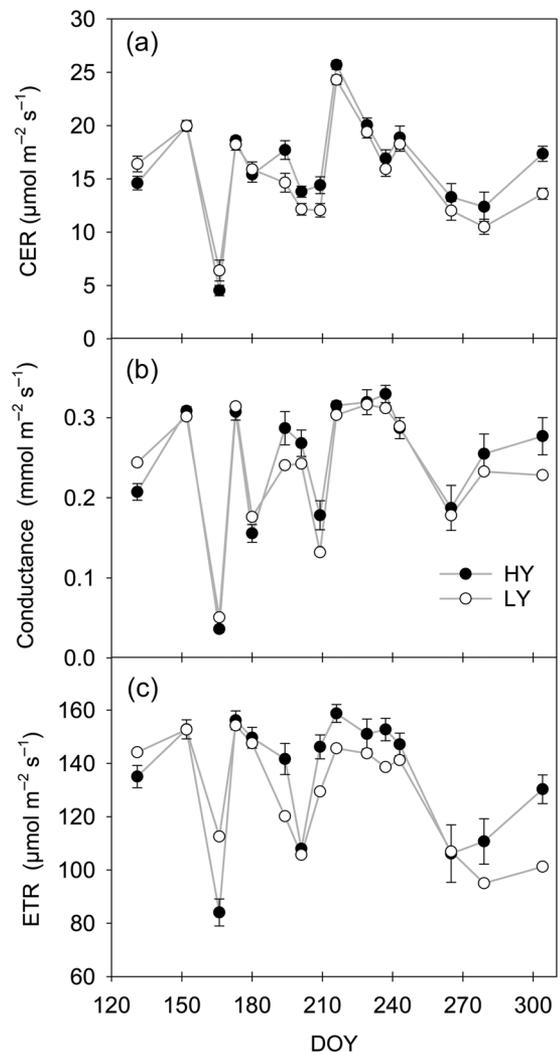

Figure 4. Time course of leaf-scale CER (a), g_s (b) and electron transfer rate (c) for olives grown in lysimeters. HY are high-yielding (>10,000 fruits) and LY are low or nonyielding trees (<10,000 fruits), respectively. Error bars are standard errors.

Direct measurements of leaf level physiology

Leaf activity, including CER, stomatal water conductivity (g_s) and ETR, fluctuated considerably, and responded with lower values during periods of water shortage. On an individual tree basis, fruit removal or thinning at any timing or severity was not accompanied by significant changes in leaf activity, measured several days or weeks afterward. Diurnal hourly measurements, aimed at elucidating possible differences in the duration of leaf activity due to alteration of source–sink relationships, did not reveal any significant differences due to fruit level or removal (data not shown). The clustering of trees by their current fruit load and SPWC (Figure 2) suggested that retrospective regrouping of the trees according to their up-to-date number of fruit might provide a more consistent view. Clustering the trees by their current fruit number into high- and low-yielding categories (HY and LY, respectively) revealed a slight, seldom significant, tendency of higher CER, g_s and ETR in HY trees between July and the final fruit harvest (Figure 4).

Water potential

The retrospective regrouping approach was employed also to the weekly measurements of midday STWP. During most of the reproductive season, HY trees displayed lower STWP values compared with LY trees (Figure 5). Nevertheless, STWP fluctuated considerably between measurements, and significant differences occurred more consistently only toward the end of season.

Fruit load and vegetative growth

Trunk cross-sectional area was employed as an indicator for the vegetative growth of the whole tree during the season. Growth rate of HY trees was significantly lower than that of LY trees only during the third study period (DOY 186–250) (Figure 6a). This observation was further confirmed using the periodic relative growth rate (RGR) of TCSA (Figure 6b). This more definitive parameter, calculated as percent of growth added per tree per period and unaffected by initial differences in the absolute dimensions of the trunk, decreased significantly in the HY trees
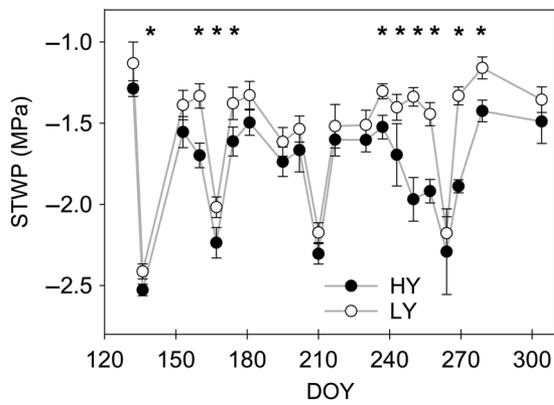
Figure 5. Time course of measured midday plant water potential (STWP) in olive trees grown in lysimeters with either current high crop load (HY, >10,000 fruits) or low/no crop load (LY, <10,000 fruits). Error bars are standard errors. Stars indicate dates with significant differences between the treatments.
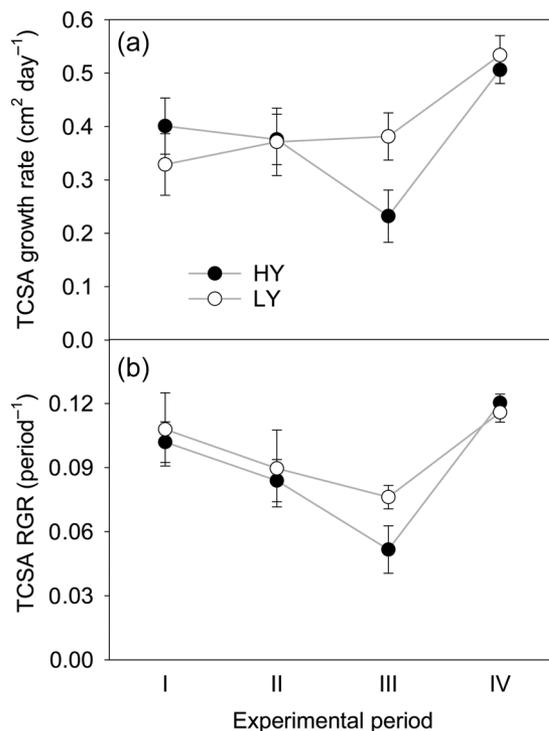

Figure 6. Growth rate of TCSA in olive trees with either current high crop load (HY, >10,000 fruits) or low/no crop load (LY, <10,000 fruits), shown as absolute values (a) or as RGR (TCSA RGR) per experimental period (b). Period I (DOY 100–140), period II (DOY 141–185), period III (DOY 186–250) and period IV (DOY 251–304). Error bars are standard errors.

from ~0.11 during the first experimental period (DOY 90–141) to <0.055 during the third period, while the reduction in the LY trees was appreciably smaller. Noteworthy is the recovery of this parameter to ~0.12 during the fourth period (DOY 251–304), among both groups of trees.

The partition of dry matter between the major aboveground organs was examined about a month after harvest. High-yielder

and LFR trees had significantly less dry trunk and limb biomass, in comparison with LY, EFR and MFR trees (Table 2). No significant differences occurred in the dry biomass of branches and leaves. The overall vegetative aboveground biomass was significantly greater for the LY, EFR and MFR trees. However, no significant difference was observed in the overall aboveground dry biomass among groups when fruit was included. A clear trade-off between fruit and vegetative growth was evident. At low fruit load or following fruit removal, vegetative growth, mainly of limbs and trunk, was stimulated. Note that under the condition of nonlimiting water supply characterizing most of the present study, all trees maintained continuous growth of leaves and branches.

Discussion

There is increasing evidence for the influence of developing fruit on the water status and water requirement of trees (Ben-Gal et al. 2011, Martín-Vertedor et al. 2011a, 2011b, Naor 2014, Sade and Moshelion 2014). This has mostly been established from indirect measurements under orchard conditions, where restricted water availability surely plays a role in water allocation between various organs and in competition between vegetative and reproductive processes. In the present study, the challenging conditions of water shortage were primarily avoided by applying water daily such that climatic and leaching requirements were satisfied and secondarily manipulated with short-term controlled drought events.

The results of the present study confirm that the dominant parameter determining tree-scale water consumption is canopy (tree) size or leaf area. Initial variability in the size of the trees in the study, in spite of their identical histories, made normalization of this parameter necessary prior to investigation of the effect of fruit load. The TCSA parameter was found to correlate very well with tree and canopy biomass and leaf area index at the end of the experiment (Figure 1). The TCSA, easily determined using lysimeters, quantitatively represents a tree's transpiring canopy and allows analysis of dynamic water consumption independent of tree size reflecting only climate and plant physiological factors.

Atmospheric demand played the most important role in changes in SPWC seen over the season. Measured daily SPWC more than doubled between winter and summer (Figure 3). Since the atmospheric demand was common to all the trees, concurrent differences in SPWC between trees must be due to differential physiological response. Unequivocally, the presence of developing fruit induced significantly greater tree-scale water consumption. This influence was not present at the beginning of the season, from flowering until final fruit set, became subsequently observable and became stronger with the progress of fruit growth and development. From DOY 185, during the periods of intensive fruit growth and oil accumulation, a clear

segregation occurred between trees displaying low and high SPWC, directly corresponding to low and high fruit loads, respectively (Figure 2). Sudden removal of fruit brought about an immediate decline in tree water consumption, which persisted until the end of the season. The later the fruit removal was executed, the greater was the response (Figure 3), indicating that factors such as fruit size or stage of development may specifically influence the governing of tree water consumption. The amount of water transpired by a fruit-loaded tree was found to be roughly 30% greater than that of a low- or nonyielding tree. While solid physiological indications exist to support hypotheses regarding the influence of fruit on the tree water status (Naor et al. 1997, 2013, Tognetti et al. 2004, Trentacoste et al. 2010, Silber et al. 2013a), to the best of our knowledge, the direct quantitative evidence presented in the current study regarding water use of fruit trees is novel.

In olives, developing fruit are known to inhibit concurrent vegetative growth (Lavee 2006). Under field conditions, fruit removal promoted subsequent vegetative growth, unless executed later than pit hardening (Dag et al. 2010). In the present study, vegetative growth was constitutive along the season, probably due to the relative young age of the trees and the non-limiting water supply. However, considerable trade-off between fruit load and vegetative development did occur, expressed by significantly greater growth rate of TCSA (Figure 6) and by the larger dry biomass of the limbs (Table 2) among low-yielding trees. This trade-off is likely even more pronounced in commercial orchards, where, in spite of prevailing water restrictions, common irrigation practices seldom consider fruit load level. Under a uniform irrigation practice, high fruit load would inhibit vegetative growth from fruit set throughout the season, during which time low-yielding trees might exhibit relatively vigorous vegetative growth. This scenario might accelerate alternate bearing. The current study joins a number of others and supports literature suggesting that fruit load must be included as a factor in irrigation scheduling (Ben-Gal et al. 2011, Dell'Amico et al. 2012, Moriana et al. 2012, Naor et al. 2013) and that, in addition to contributing to significant water savings, irrigation practices that consider fruit load may be a useful means reducing irregular bearing in olives.

Beyond such practical considerations, the question of how developing fruit influence tree water requirements can be considered. Possible mechanisms include stomatal response to water balance and alteration of the soil–plant–atmospheric continuum, influence on carbon source–sink relationships, dynamic progression from isohydric to anisohydric stomatal regulation or signals from fruit promoting changes in hydraulic properties of vascular tissues and tree organs.

Unlike leaves that possess a large surface to volume ratio and are rich with stomata, the fruit is a spheroid displaying much smaller specific surface area. A few active stomata are indeed present on the fruit surface at an early stage of development, but these are quickly covered with a waxy cuticle. Thus, significant gas and water exchange between the fruit and its environment does not occur during most of the fruit development period (Proietti et al. 1999), and therefore, fruit do not directly contribute to tree transpiration or tree-scale water balance.

Developing fruit function as a strong sink for photoassimilates. Theoretically, the demands by heavy fruit load may exert intensified foliar activity, exhibited by enhanced CER or extended periods of photosynthetic activity. Enhanced CER would require some increase in g_s, which might explain the escalated transpiration occurring under high fruit loads. Noteworthy, however, is the rather weak relationships between g_s and CER at the upper range of g_s (Fernández 2014). Nevertheless, in the present study, CER values as well as g_s did not vary significantly between high and low fruit loads (Figure 4). Also, diurnal examinations of these parameters (data not shown) did not provide evidence for extended foliar activity under high fruit load. These results are in agreement with previous studies in olive (Proietti 2001, Hagidimitriou and Pontikis 2005, Proietti et al. 2006), which showed that leaf-to-fruit ratio scarcely affected CER and g_s. Conversely, Martín-Vertedor et al. (2011a) were able to show that under medium or high crop load, g_s increased by an average of 17% over trees that did not have fruits. We recognize that the data regarding leaf-scale photosynthesis and transpiration in the current study, taken midday on diagnostic leaves, were not sufficient to absolutely negate possible fruit load influence on the processes and their diurnal dynamics.

There are several explanations for the difficulty in obtaining the expected differences in olive leaf activity. Discrete instantaneous g_s measurements would always be subject to many environmental and intrinsic influences, including the diurnal dynamics of exposure to sunlight, temperature, vapor pressure deficit (VPD) and leaf age. A mature olive tree carries a huge number of small leaves, the variability among which may be immense at any given moment. Elucidating the effect of a single factor under field conditions from only a few instantaneous measurements would be statistically rather challenging, due to the very low signal-to-noise ratio expected. Therefore, even if it exists, a direct influence of fruit on g_s may be difficult to capture via typical measurement methods. Additionally, Fernández et al. (2011) showed that, under typical semiarid summer conditions, $g_{s\text{-max}}$ was usually reached in the morning, much earlier than the diurnal climax of plant transpiration (T_a). Similarly, maximum sap flow rates are recorded in the afternoon, while stomatal closure begins much earlier, in the morning (Moreno et al. 1996). This is because T_a, and consequently, the sap flow in the trunk, is driven mainly by VPD, following its daily pattern (Tognetti et al. 2009, Diaz-Espejo et al. 2012). While increasing VPD also induces earlier stomatal closure, the reducing effect of decreased g_s is smaller than the enhancement of T_a by high VPD (Fernández 2014). Thus, the linkage between g_s and T_a, especially concerning instantaneous measurements, was far from straightforward

during the present study. Whole-tree performance was, therefore, preferably evaluated by direct integrative measurement of T_a.

In the long term, however, g_s may play a significant role in adjusting tree water status. Tardieu and Simonneau (1998) distinguished between isohydric species, where stomatal regulation maintains a fairly consistent minimum leaf water potential (ψ_l) from day to day, and anisohydric species, where ψ_l markedly decreases with changes in evaporative demand. Klein (2014) recently suggested a continuum rather than a dichotomy between isohydric and anisohydric behaviors. Moreover, the mode of stomatal regulation (i.e., isohydric/anisohydric) has been shown to vary over the course of a growing season in a given species. Some grapevine cultivars, for instance, show dynamic stomatal sensitivity and can switch from isohydric-like behavior to anisohydric-like behavior in response to changing environmental conditions (Rogiers et al. 2012, Zhang et al. 2012).

Cuevas et al. (2010) reported that olives showed near-isohydric behavior, similar to that reported for other Mediterranean woody crops (Schultz 2003). Analogous to several other fruit tree species (e.g., grapevine, apple and avocado) reported to change their 'risk-management strategies' (Palmer 1992, Naor et al. 1997, 2008, Silber et al. 2013a), olives have been shown to exhibit higher g_s and higher CO_2 assimilation rate under heavy crop load, although these effects were more pronounced under deficit irrigation than in well-irrigated trees (Naor et al. 2013). Moreover, solid evidence exists concerning the influence of fruit load in olives on midday water potential, a widely accepted integrative parameter of tree water status. As shown here as well (Figure 5), high crop load is significantly associated with a decrease in midday plant (stem) water potential (Sadras and Trentacoste 2011, Naor et al. 2013). This behavioral change implies a shift in hydraulic regulation as a function of sink demand.

Olives generally display low hydraulic conductivity (Larsen et al. 1989, Bongi and Palliotti 1994) and are able to withstand water potentials below turgor-loss point with minor seasonal xylem embolism (Torres-Ruiz et al. 2013). Subsequently, under different water regimes, olives display differences in xylem structure and function (López-Bernal et al. 2010, Rossi et al. 2013). In semiarid regions, these traits support survival of individual trees. Nevertheless, the emergence of the reproductive phase necessitates an opposite evolutionary strategy, in which water and nutrient availability should be enhanced to furnish the development of seeds and complete the reproduction process. In fact, the full-bloom and fruit development phases have been found to be the most sensitive periods for water stress in olive trees (Tognetti et al. 2005, Moriana et al. 2012). Therefore, some aptitude to trade-off between high hydraulic conductance and avoidance of embolism (Martínez-Vilalta et al. 2002, Hacke et al. 2006) is required. Diaz-Espejo et al. (2012) suggested that regulating signals other than simple hydraulics were potentially

involved in determining plant water conductance in olives, and that these signals were themselves controlled by something other than soil water status. Possibly these signals emerge from developing fruit.

Plant water channels, aquaporins (AQPs), are understood to play significant roles in controlling plant water status, hydraulic conductivity, membrane osmotic permeability and stomatal regulation (Kaldenhoff et al. 2007, Shatil-Cohen et al. 2011, Prado and Maurel 2013, Li et al. 2014, Moshelion et al. 2015). Aquaporins are subject to rapid, substantial and stable shoot-to-root signals, regulating root hydraulic conductivity (Vandeleur et al. 2014). Similarly, developing fruit may govern AQP expression and activity in remote plant organs (Sade and Moshelion 2014). Developing fruit, via the excretion of plant hormones, provoke and govern the construction of supporting vascular systems (Nitsch 1952, Crane 1964, Aloni 1987, Bustan et al. 1995, Ozga and Reinecke 2003, Else et al. 2004). Hormonal factors may also regulate the functioning of the fruit vascular routes, ensuring sufficient supply of water and nutrients. Significant differences occurring in AQP expression between low- and high-yielding olive trees (Turktas et al. 2013) may support this view.

High turgor pressure is essential for the growth of plant organs, particularly of fruit. Under Mediterranean summer conditions, turgor pressure during the day tends to be very low. Therefore, fruit growth is commonly limited to periods after nocturnal water recovery and turgor pressure revival. Rapid reclamation of plant water status following midday decline would extend the prospective growth period, benefiting growing organs. The rate of nocturnal water recovery depends on environmental water status (soil water availability and VPD), plant capacity for water storage (Moreno et al. 1996, Fernández et al. 2006) and on xylem water conductance. Sap flow at night is known to occur in olive, accounting for significant nocturnal water recovery (Fernández et al. 2008). Developing fruit likely act, via hormones and AQPs, to enhance both xylem water conductance and plant capacity for water storage. While a clear benefit would be ascertained by fruit growth at night, enhanced xylem water conductance likely also leads to increased transpiration and consequent lower STWP.

Conclusions

Under the normally nonrestrictive water conditions that prevailed in the present study, constitutive vegetative growth suggests that carbon sources were not limited. Symptoms of carbon sink limitation, such as declined CER and g_s, expected in response to fruit removal, were for the most part insignificant, possibly due to alternative sink demands. Nevertheless, fruit load had a significant effect on tree water potential and an even greater effect on tree-scale water consumption, which was ~30% higher in fruit-loaded trees and responded dramatically to fruit removal. Mechanisms explaining the role of fruit on water consumption

likely involve signaling and changing hydraulic properties of vascular tissues and tree organs.

Conflict of interest

None declared.

Funding

References

Agam N, Cohen Y, Berni JAJ, Alchanatis V, Kool D, Dag A, Yermiyahu U, Ben-Gal A (2013) An insight to the performance of crop water stress index for olive trees. Agric Water Manag 118:79–86.

Allen RG, Pereira LS, Raes D, Smith M (1998) Crop evapotranspiration—guidelines for computing crop water requirements. FAO Irrigation and Drainage Paper 56. UN-FAO, Rome.

Aloni R (1987) Differentiation of vascular tissues. Annu Rev Plant Physiol 38:179–204.

Avery DJ (1975) Effects of fruits on photosynthetic efficiency. In: Pereira HC (ed) Climate and the orchard. CAB, Farnham Royal, Slough, UK, pp 110–112.

Ben-Gal A, Shani U (2002) A highly conductive drainage extension to control the lower boundary condition of lysimeters. Plant Soil 239:9–17.

Ben-Gal A, Kool D, Agam N et al. (2010) Whole-tree water balance and indicators for short-term drought stress in non-bearing 'Barnea' olives. Agric Water Manag 98:124–133.

Ben-Gal A, Yermiyahu U, Zipori I, Presnov E, Hanoch E, Dag A (2011) The influence of bearing cycles on olive oil production response to irrigation. Irrigation Sci 29:253–263.

Berman ME, DeJong TM (1996) Water stress and crop load effects on fruit fresh and dry weights in peach (Prunus persica). Tree Physiol 16:859–864.

Bongi G, Palliotti A (1994) Olive. In: Schaffer B, Andersen PC (eds) Handbook of environmental physiology of fruit crops. Volume I: temperate crops. CRC Press, Inc., Boca Raton, FL, pp 165–187.

Bustan A, Goldschmidt EE (1998) Estimating the cost of flowering in a grapefruit tree. Plant Cell Environ 21:217–224.

Bustan A, Erner Y, Goldschmidt EE (1995) Interactions between developing citrus fruits and their supportive vascular system. Ann Bot 76:657–666.

Bustan A, Avni A, Lavee S, Zipori I, Yeselson Y, Schaffer AA, Riov J, Dag A (2011) Role of carbohydrate reserves in yield production of intensively cultivated oil olive (Olea europaea L.) trees. Tree Physiol 31:519–530.

Castillo-Llanque F, Rapoport H (2009) Identifying the location of olive fruit abscission. Sci Hortic 120:292–295.

Conejero W, Ortuño MF, Mellisho CD, Torrecillas A (2010) Influence of crop load on maximum daily trunk shrinkage reference equations for irrigation scheduling of early maturing peach trees. Agric Water Manag 97:333–338.

Connor DJ (2005) Adaptation of olive (Olea europaea L.) to water-limited environments. Aust J Agric Res 56:1181–1189.

Crane J (1964) Growth substances in fruit setting and development. Annu Rev Plant Physiol 15:303–326.

Cuevas MV, Torres-Ruiz JM, Álvarez R, Jiménez MD, Cuerva J, Fernández JE (2010) Assessment of trunk diameter variation derived indices as water stress indicators in mature olive trees. Agr Water Manage 97:1293–1302.

Dag A, Bustan A, Avni A, Zipori I, Lavee S, Riov J (2010) Timing of fruit removal affects concurrent vegetative growth and subsequent return bloom and yield in olive (Olea europaea L.). Sci Hortic 123:469–472.

DeJong TM (1986) Fruit effects on photosynthesis in Prunus persica. Physiol Plant 66:149–153.

Dell'Amico J, Moriana A, Corell M, Girón IF, Morales D, Torrecillas A, Moreno F (2012) Low water stress conditions in table olive trees (Olea europaea L.) during pit hardening produced a different response of fruit and leaf water relations. Agric Water Manag 114:11–17.

Diaz-Espejo A, Buckley TN, Sperry JS et al. (2012) Steps toward an improvement in process-based models of water use by fruit trees: a case study in olive. Agric Water Manag 114:37–49.

Else MA, Stankiewicz-Davies AP, Crisp CM, Atkinson CJ (2004) The role of polar auxin transport through pedicels of Prunus avium L. in relation to fruit development and retention. J Exp Bot 55:2099–2109.

Fernández JE (2014) Understanding olive adaptation to abiotic stresses as a tool to increase crop performance. Environ Exp Bot 103:158–179.

Fernández JE, Diaz-Espejo A, Infante JM, Durán P, Palomo MJ, Chamorro V, Girón IF, Villagarcía L (2006). Water relations and gas exchange in olive trees under regulated deficit irrigation and partial root zone drying. Plant Soil 284:273–291.

Fernández JE, Diaz-Espejo A, d'Andria R, Sebastiani L, Tognetti R (2008) Potential and limitations of improving olive orchard design and management through modelling. Plant Biosyst 142:130–137.

Fernández JE, Moreno F, Martín-Palomo MJ, Cuevas MV, Torres-Ruiz JM, Moriana A (2011) Combining sap flow and trunk diameter measurements to assess water needs in mature olive orchards. Environ Exp Bot 72:330–338.

Gifford RM, Evans LT (1981) Photosynthesis, carbon partitioning, and yield. Annu Rev Plant Physiol 32:485–509.

Goldschmidt EE, Golomb A (1982) The carbohydrate balance of alternate-bearing citrus trees and the significance of reserves for flowering and fruiting. J Am Soc Hortic Sci 107:206–208.

Goldschmidt EE, Huber SC (1992) Regulation of photosynthesis by end-product accumulation in leaves of plants storing starch, sucrose, and hexose sugars. Plant Physiol 99:1443–1448.

Grattan SR, Berenguer MJ, Connell JH, Polito VS, Vossen PM (2006) Olive oil production as influenced by different quantities of applied water. Agric Water Manag 85:133–140.

Guichard S, Gary C, Leonardi C, Bertin N (2005) Analysis of growth and water relations of tomato fruits in relation to air vapor pressure deficit and plant fruit load. J Plant Growth Regul 24:201–213.

Hacke UG, Sperry JS, Wheeler JK, Castro L (2006) Scaling of angiosperm xylem structure with safety and efficiency. Tree Physiol 26:689–701.

Hagidimitriou M, Pontikis CA (2005) Seasonal changes in CO_2 assimilation in leaves of five major Greek olive cultivars. Sci Hortic 104:11–24.

Haouari A, Van Labeke M-C, Steppe K, Ben Mariem F, Braham M, Chaieb M (2013) Fruit thinning affects photosynthetic activity, carbohydrate levels, and shoot and fruit development of olive trees grown under semiarid conditions. Funct Plant Biol 40:1179–1186.

Huberman M, Goren R, Zamski E (1983) Anatomical aspects of hormonal regulation of abscission in citrus—the shoot-peduncle abscission zone in the non-abscising stage. Physiol Plant 59:445–454.

Iniesta F, Testi L, Orgaz F, Villalobos FJ (2009) The effects of regulated and continuous deficit irrigation on the water use, growth and yield of olive trees. Eur J Agron 30:258–265.

Intrigliolo DS, Castel JR (2007) Crop load affects maximum daily trunk shrinkage of plum trees. Tree Physiol 27:89–96.

Kaldenhoff R, Bertl A, Otto B, Moshelion M, Uehlein N (2007) Characterization of plant aquaporins. Methods Enzymol 428:505–531.

Klein T (2014) The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. Funct Ecol 28:1313–1320.

Körner C (2003) Carbon limitation in trees. J Ecol 91:4–17.

Larsen FE, Higgins SS, Al-Wir A (1989) Diurnal water relations of apple, apricot, grape, olive and peach in an arid environment (Jordan). Scientia Horticulturae 39:211–222.

Lavee S (2006) Biennial bearing in olive (Olea europaea L.). Olea FAO Olive Network 25:5–13.

Lavee S (2011) The revolutionary impact of introducing irrigation-intensification to the olive oil industry. Acta Hortic 21–30. doi:10.17660/ActaHortic.2011.888.1

Lavee S, Nashef M, Wodner M, Harshemesh H (1990) The effect of complementary irrigation added to old olive trees (Olea europaea L.) cv Souri on fruit characteristics, yield and oil production. Adv Hortic Sci 4:135–138.

Li G, Santoni V, Maurel C (2014) Plant aquaporins: roles in plant physiology. Biochim Biophys Acta 1840:1574–1582.

López-Bernal Á, Alcántara E, Testi L, Villalobos FJ (2010) Spatial sap flow and xylem anatomical characteristics in olive trees under different irrigation regimes. Tree Physiol 30:1536–1544.

Martín-Vertedor AI, Pérez-Rodrígue JM, Prieto-Losada H, Fereres-Castiel E (2011a) Interactive responses to water deficits and crop load in olive (Olea europaea L., cv. Morisca) I.—growth and water relations. Agric Water Manag 98:941–949.

Martín-Vertedor AI, Pérez-Rodrígue JM, Prieto-Losada H, Fereres-Castiel E (2011b) Interactive responses to water deficits and crop load in olive (Olea europaea L., cv. Morisca). II: water use, fruit and oil yield. Agric Water Manag 98:950–958.

Martínez-Vilalta J, Prat E, Oliveras I, Piñol J (2002) Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. Oecologia 133:19–29.

Moreno F, Fernández JE, Clothier BE, Green SR (1996) Transpiration and root water uptake by olive trees. Plant Soil 184:85–96.

Moriana A, Orgaz F, Pastor M, Fereres E (2003) Yield responses of a mature olive orchard to water deficit. J Am Soc Hortic Sci 128:425–431.

Moriana A, Pérez-López D, Prieto MH, Ramírez-Santa-Pau M, Pérez-Rodrígue JM (2012) Midday stem water potential as a useful tool for estimating irrigation requirements in olive trees. Agric Water Manag 112:43–54.

Moshelion M, Halperin O, Wallach R, Oren R, Way DA (2015) Role of aquaporins in determining transpiration and photosynthesis in water-stressed plants: crop water-use efficiency, growth and yield. Plant Cell Environ 38:1785–1793.

Muller B, Pantin F, Génard M, Turc O, Freixes S, Piques M, Gibon Y (2011) Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs. J Exp Bot 62:1715–1729.

Naor A (2006) Irrigation scheduling and evaluation of tree water status in deciduous orchards. Janick J (ed) Horticultural Reviews. Vol. 32, John Wiley & Sons, Oxford, UK, pp 112–165.

Naor A (2014) Crop load and irrigation interactions—a new dimension of RDI. Acta Hortic 113–119. doi:10.17660/ActaHortic.2014.1038.12

Naor A, Gal Y, Bravdo B (1997) Crop load affects assimilation rate, stomatal conductance, stem water potential and water relations of field-grown Sauvignon blanc grapevines. J Exp Bot 48:1675–1680.

Naor A, Naschitz S, Peres M, Gal Y (2008) Responses of apple fruit size to tree water status and crop load. Tree Physiol 28:1255–1261.

Naor A, Schneider D, Ben-Gal A, Zipori I, Dag A, Kerem Z, Birger R, Peres M, Gal Y (2013) The effects of crop load and irrigation rate in the oil accumulation stage on oil yield and water relations of 'Koroneiki' olives. Irrigation Sci 31:781–791.

Nitsch JP (1952) Plant hormones in the development of fruits. Q Rev Biol 27:33–57.

Ozga JA, Reinecke DM (2003) Hormonal interactions in fruit development. J Plant Growth Regul 22:73–81.

Palmer JW (1992) Effects of varying crop load on photosynthesis, dry matter production and partitioning of Crispin/M.27 apple trees. Tree Physiol 11:19–33.

Prado K, Maurel C (2013) Regulation of leaf hydraulics: from molecular to whole plant levels. Front Plant Sci 4:255.

Proietti P (2001) Effect of fruiting on leaf gas exchange in olive (Olea europaea L.). Photosynthetica 38:397–402.

Proietti P, Famiani F, Tombesi A (1999) Gas exchange in olive fruit. Photosynthetica 36:423–432.

Proietti P, Nasini L, Famiani F (2006) Effect of different leaf-to-fruit ratios on photosynthesis and fruit growth in olive (Olea europaea L.). Photosynthetica 44:275–285.

Rapoport HF, Rallo L (1991) Postanthesis flower and fruit abscission in 'Manzanillo' olive. J Am Soc Hortic Sci 116:720–723.

Rivas F, Erner Y, Alós E, Juan M, Almela V, Agusti M (2006) Girdling increases carbohydrate availability and fruit-set in citrus cultivars irrespective of parthenocarpic ability. J Hortic Sci Biotechnol 81:289–295.

Rogiers SY, Greer DH, Hatfield JM, Hutton RJ, Clarke SJ, Hutchinson PA, Somers A (2012) Stomatal response of an anisohydric grapevine cultivar to evaporative demand, available soil moisture and abscisic acid. Tree Physiol 32:249–261.

Rossi L, Sebastiani L, Tognetti R, d'Andria R, Morelli G, Cheubini P (2013) Tree-ring wood anatomy and stable isotopes show structural and functional adjustments in olive trees under different water availability. Plant Soil 372:567–579.

Sade N, Moshelion M (2014) The dynamic isohydric–anisohydric behavior of plants upon fruit development: taking a risk for the next generation. Tree Physiol 34:1199–1202.

Sadras VO, Trentacoste ER (2011) Phenotypic plasticity of stem water potential correlates with crop load in horticultural trees. Tree Physiol 31:494–499.

Schultz HR (2003) Differences in hydraulic architecture account for near-isohydric and anisohydric behaviour of two field-grown Vitis vinifera L. cultivars during drought. Plant Cell Environ 26:1393–1405.

Serra-Majem L, Ngo de la Cruz J, Ribas L, Tur JA (2003) Olive oil and the Mediterranean diet: beyond the rhetoric. Eur J Clin Nutr 57:S2–S7.

Shackel KA, Ahmadi H, Biasis W et al. (1997) Plant water status as an index of irrigation need in deciduous fruit trees. HortTechnology 7:23–29.

Shatil-Cohen A, Attia Z, Moshelion M (2011) Bundle-sheath cell regulation of xylem–mesophyll water transport via aquaporins under drought stress: a target of xylem-borne ABA? Plant J 67:72–80.

Silber A, Israeli Y, Levi M et al. (2013a) The roles of fruit sink in the regulation of gas exchange and water uptake: a case study for avocado. Agric Water Manag 116:21–28.

Silber A, Naor A, Israeli Y, Assouline S (2013b) Combined effect of irrigation regime and fruit load on the patterns of trunk-diameter variation of 'Hass' avocado at different phenological periods. Agric Water Manag 129:87–94.

Syvertsen JP, Goñi C, Otero A (2003) Fruit load and canopy shading affect leaf characteristics and net gas exchange of 'Spring' navel orange trees. Tree Physiol 23:899–906.

Tardieu F, Simonneau T (1998) Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. J Exp Bot 49:419–432.

Tognetti R, d'Andria R, Morelli G, Calandrelli D, Fragnito F (2004) Irrigation effects on daily and seasonal variations of trunk sap flow and leaf water relations in olive trees. Plant Soil 263:249–264.

Tognetti R, d'Andria R, Morelli G, Alvino A (2005) The effect of deficit irrigation on seasonal variations of plant water use in Olea europaea L. Plant Soil 273:139–155.

Tognetti R, Giovannelli A, Lavini A, Morelli G, Fragnito F, d'Andria R (2009) Assessing environmental controls over conductances through the soil–plant–atmosphere continuum in an experimental olive tree plantation of southern Italy. Agric For Meteorol 149:1229–1243.

Torres-Ruiz JM, Diaz-Espejo A, Morales-Sillero A, Martín-Palomo MJ, Mayr S, Beikircher B, Fernández JE (2013) Shoot hydraulic characteristics, plant water status and stomatal response in olive trees under different soil water conditions. Plant Soil 373:289–308.

Trentacoste ER, Puertas CM, Sadras VO (2010) Effect of fruit load on oil yield components and dynamics of fruit growth and oil accumulation in olive (Olea europaea L.). Eur J Agron 32:249–254.

Tripler E, Shani U, Ben-Gal A, Mualem Y (2012) Apparent steady state conditions in high resolution weighing-drainage lysimeters containing date palms grown under different salinities. Agric Water Manag 107:66–73.

Turktas M, Inal B, Okay S, Erkilic EG, Dundar E, Hernandez P, Dorado G, Unver T (2013) Nutrition metabolism plays an important role in the alternate bearing of the olive tree (Olea europaea L.). PLoS One 8:e59876. doi:10.1371/journal.pone.0059876

Vandeleur RK, Sullivan W, Athman A, Jordans C, Gilliham M, Keiser BN, Tyreman SD (2014) Rapid shoot-to-root signalling regulates root hydraulic conductance via aquaporins. Plant Cell Environ 37:520–538.

Wünsche JN, Ferguson IB (2005) Crop load interactions in apple. In: Janick J (ed) Horticultural reviews 31. John Wiley & Sons Inc., Hoboken, NJ, pp 231–290.

Zhang Y, Oren R, Kang S (2012) Spatiotemporal variation of crownscale stomatal conductance in an arid Vitis vinifera L. cv. Merlot vineyard: direct effects of hydraulic properties and indirect effects of canopy leaf area. Tree Physiol 32:262–279.

Zucconi F, Monselise SP, Goren R (1978) Growth abscission relationships in developing orange fruit. Sci Hortic 9:137–146.