ORIGINAL PAPER

Deficit irrigation and warming during the late winter and spring affect vegetative growth and reproductive development in young olive trees

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Abstract

To better understand the implications of climate change, the combined responses of olive trees to irrigation amount and warming need to be examined. Thus, the objective was to evaluate the effects of moderate deficit irrigation and warming during late winter and spring on vegetative growth and biomass, full bloom timing and intensity, and yield components in young olive trees. Two three month-long experiments were conducted using open top chambers with four treatment combinations: 100% irrigation with a control temperature; 100% irrigation with 4 °C warming; 50% irrigation with a control temperature; and 50% irrigation with 4 °C warming. The trees were potted two-year-old, cv. Arbequina trees in the 2018 experiment and three-year-old, cv. Coratina trees in the 2019 experiment. Flowering was low in the young cv. Arbequina trees in 2018, but it was much greater in the older cv. Coratina trees in 2019. Overall, lower flowering intensity and fruit set or more partheno-carpic fruit contributed to less viable fruit number with warming. These reproductive variables were less affected by deficit irrigation. In contrast, shoot growth and vegetative biomass were decreased by deficit irrigation in cv. Arbequina (2018) when fruit number was low in all trees with less response due to warming. In cv. Coratina (2019), the lower fruit number in warmed compared to control trees contributed to greater individual fruit weight at the end of the experimental period, and few significant effects of either deficit irrigation or warming on shoot growth were observed. Fruit yield was greater in the well-irrigated, temperature control than in the other treatment combinations in cv. Arbequina, while warming reduced fruit yield in cv. Coratina. From a production perspective, it does not appear that many early reproductive responses to warming can be easily counteracted by adjusting irrigation. Further studies with more mature trees and cultivars over several growing seasons are recommended.

Introduction

Irrigation and air temperature are important factors for olive production in arid and semi-arid regions (Fernández 2014; Brito et al. 2019; Ben-Ari et al. 2021). Although olive has been traditionally cultivated in the Mediterranean Basin under dry land conditions, irrigation is a common management tool in modern high- and super-high density orchards

(Connor et al. 2014; Ahumada-Orellana et al. 2017; Ferrara et al. 2023). Up to a certain threshold, irrigation improves fruit and oil yields, and may mitigate adverse conditions due to climate change such as less rainfall and warming (Fraga et al. 2020). Furthermore, the continuing expansion of olive production into new regions with different temperature and rainfall regimes than that of the Mediterranean requires greater knowledge of how and when to irrigate olive trees (Torres et al. 2017).

The main olive production region in Argentina is located in the central western and northwestern part of the country, and its continental climate is markedly different than that of the Mediterranean Basin (Searles et al. 2011). Mean annual maximum temperatures are high (26–28 °C) with rainfall (100 to 400 mm per year) being concentrated in the summer rather than the fall and winter as occurs in Mediterranean climates. Additionally, moderate winter and warm spring temperatures lead to early vegetative growth and reproductive development (Correa-Tedesco et al. 2010; Rondanini

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et al. 2014; Hamze et al. 2022). For these reasons, irrigation is frequent during the winter and spring, and expected warming during this period could have negative impacts on olive production in the region (Miserere et al. 2019a, 2021, 2022).

Vegetative growth and reproductive development overlap during much of the spring in olive trees (Smith and Samach 2013; Rosati et al. 2018; Zucchini et al. 2023). Apical shoot growth begins when the air temperature increases at the end of winter (López-Bernal et al. 2020) and decreases in the late spring when fruit growth becomes a strong competing carbon sink (Fernández et al. 2015). However, if fruit load is low, shoot growth can extend throughout much of the year (Dag et al. 2010). Reproductive bud burst occurs towards the end of winter following chilling accumulation (Sanz-Cortés et al. 2002; Haberman et al. 2017), and is followed by several weeks of thermal time accumulation until full bloom occurs during the spring (De Melo-Abreu et al. 2004). Flowering intensity is a major yield determinant despite olive trees often producing a very large number of flowers (Lavee 1996; Famiani et al. 2019). Fruit set is initially very high, but competition for photoassimilates leads to considerable fruit abortion following full bloom (Rallo and Fernández-Escobar 1985). Additionally, fruit set is often reduced under very low or high temperatures, and temperature extremes can also lead to the formation of small parthenocarpic (i.e., seedless) fruit known as shot berries in some cultivars (Cuevas et al. 1994; Koubouris et al. 2010). After fruit set, the number of commercially viable fruit, individual fruit weight, and oil concentration (%) become the major components that contribute to final yield, which occurs five to six months after full bloom.

Several winter and spring deficit irrigation studies have evaluated shoot growth, flowering, and yields in olive trees. A severe deficit irrigation (25% of crop evapotranspiration; ETc) during mid-winter had no impact on full bloom in potted olive trees, but a similar deficit during early inflorescence formation at the end of winter reduced the number of inflorescences and flowers; and thus, fruit number per tree (Rapoport et al. 2012). Furthermore, decreases in shoot growth, flowering intensity, fruit set, and fruit number were observed with significant reductions in final yield when irrigation less than 75% of ETc was applied for an extended 4-month period prior to bloom in a mature orchard in central western Argentina (Pierantozzi et al. 2014). Deficit irrigation during bloom can not only reduce yields due to lower fruit number in the same season, but concurrent reductions in shoot growth can reduce yield the following growing season due to the formation of fewer nodes and thus fewer potentially reproductive lateral buds (Hueso et al. 2021). On the other hand, spring deficit irrigation has been found to improve yields over several seasons if vegetative vigor is excessive after moderate or severe hedgerow pruning in super-high density orchards (Trentacoste et al. 2019).

In comparison to deficit irrigation, there is little information of how air temperatures in late winter and spring affects vegetative biomass production and final yield (Ben-Ari et al. 2021). The minimum growth temperature of shoots and fruit has been estimated to be around 15 °C under field conditions (Pérez-López et al. 2008). Although maximum growth temperature thresholds are largely unknown, a constant temperature of 37 °C significantly reduced vegetative biomass accumulation relative to 25 °C in young olive plants grown in growth chambers (Benlloch-González et al. 2016). In contrast, outdoor warming (+ 4 °C) of large olive trees over three years in open top chambers (OTCs) promoted trunk and branch growth in southern Spain (Benlloch-González et al. 2019). This increase was likely related to more available carbon for vegetative growth due to lower fruit set and fruit number and final yields under the experimental warming conditions (Benlloch-González et al. 2018, 2019). In these same studies, flowering intensity was not affected, but full bloom was about 20 days earlier. Warming (3–4 °C) after final fruit set during the oil accumulation phase reduced individual fruit weight, fruit oil concentration, and oil yields in young olive trees grown in OTCs in northwestern Argentina (Miserere et al. 2022, 2023). Similar to the southern Spain studies, warming increased vegetative growth when measured as the net leaf area accumulation. However, flowering intensity was reduced the spring following the warming period, which lasted from early summer until mid-fall.

To better understand the consequences of climate change, studies examining the combined responses of olive trees to water stress and increased air temperature of different duration and magnitude are needed (Suzuki et al. 2014). Both a short, two hours long heat shock in a growth chamber and a several days long, natural heat wave sharply reduced net leaf photosynthesis in well-irrigated plants, but photosynthesis was not further reduced by the heat shock or heat wave in plants under severe water stress (Haworth et al. 2018; Araújo et al. 2019). In contrast, a recent study of moderate deficit irrigation and prolonged warming (+ 4 °C) in late winter and spring found that net photosynthesis was consistently decreased by deficit irrigation, but the response to warming was temperature dependent (Iglesias et al. 2023). Additionally, midday stem water potential was reduced by both deficit irrigation and warming in that study.

There is currently no information as to how vegetative growth and reproductive development will be affected by combined deficit irrigation and warming in olive trees. A recent meta-analysis of 37 studies including woody and herbaceous species found that both drought and warming reduced aboveground vegetative biomass in an additive manner (Wilschut et al. 2022). Given the apparent sensitivity of reproductive development in olive trees to water stress and high air temperatures separately (e.g., Cuevas

et al. 1994; Rapoport et al. 2012), fruit and oil yield may be particularly affected by these factors when combined. The objective of this study was to evaluate the effects of a moderate deficit irrigation (50% of water consumed) and warming (+ 4 °C) during late winter and spring on vegetative growth and biomass, full bloom timing and intensity, and yield components in young olive trees.

Materials and methods

Plant material

The biomass and reproductive measurements reported here are part of a larger warming study described by Iglesias et al. (2023) at the CRILAR-CONICET experimental field station in La Rioja, Argentina (28° 48′ S latitude, 66° 56′ W longitude; 1325 m above sea level). The region is arid with average annual maximum and minimum temperatures of approximately 27 and 13 °C; respectively, and an annual reference evapotranspiration of 1600 mm (Torres et al. 2017). Annual rainfall at the experimental site is 150 mm (Searles et al. 2011). Due to mild winters and warm temperatures in early spring, the crop phenology advances rapidly including full separation of the first pair of leaves (BBCH 11) in late winter and full bloom (BBCH 65) several weeks later (Hamze et al. 2022). The abbreviation BBCH (Biologische Bundesanstalt, Bundessortenamt, Chemische Industrie) refers to the phenological scale developed for olive by Sanz-Cortés et al. (2002).

The responses to irrigation and increased temperature were assessed in young olive trees in the late winter and spring of 2018 and 2019 (i.e., mid-August to late November) inside open top chambers. The trees were two-year-old, cv. Arbequina trees in the 2018 experiment and three-year-old, cv. Coratina trees in the 2019 experiment. These cultivars are common to commercial orchards in both the Mediterranean Basin and Argentina. The trees were prepared from cuttings by a local nursery (San Gabriel; La Rioja, Argentina), and transplanted at the field station into 30 L plastic pots in the spring of 2017. The soil substrate was composed of sand, peat, and perlite (1: 1: 0.1, v/v) to obtain high water retention. The trees were then grown outdoors at the field station until the experiment. The leaf area per tree at the beginning of the treatments was 0.35 m^2 and 1.05 m^2 for 2018 and 2019, respectively. The cv. Arbequina was not chosen for the 2019 experiment due to low flowering intensity the previous year and the availability of larger, older cv. Coratina trees in 2019.

Experimental design and treatments

The experiment had a completely randomized design with four treatment combinations including: 100% irrigation with a near-ambient, air temperature control (100 Tc); 100% irrigation with 4 °C warming of the air temperature above that of the control (100 T+); 50% irrigation with a near-ambient, air temperature control (50 Tc); and 50% irrigation with 4 °C warming of the air temperature above that of the control (50 T+). These combinations were implemented within 16 OTCs including four replicate OTCs for each irrigation and air temperature combination and two sub-replicate trees in each OTC. Each tree was placed below the soil surface within a 30 cm-deep well to reduce soil and root heating. Soil temperature in the pots measured at 10 cm below the soil surface with thermocouples was about 10 ºC less than air temperature during the daytime, and was consistently less in the controls than in the warmed treatments.

Warming was initiated in late winter at the beginning of leaf growth (i.e., the first pair of leaves starting to separate; BBCH 07) prior to any visual observation of lateral, reproductive buds opening (BBCH 53) on about August 10th of each year. According to the methodology of De Melo-Abreu et al. (2004), the accumulated chilling units during the fall and winter were 931 in 2018 and 1200 in 2019 at the beginning of experimental warming. Irrigation treatments started about 10 days later to ensure correct functioning of the warming system. A given OTC received either the near-ambient, control temperature (Tc) or was warmed to a target temperature of 4 °C more than the Tc OTCs. The dimensions of the cube-shaped OTCs were 2.0 m × 1.5 m × 1.5 m, and the side walls were covered by 150 μm thick polyethylene plastic (Premium Thermal Agrotileno PLDT221510, AgroRedes, Argentina). A walk-in door on one side provided access to the trees for measurements. Each Tc OTC had a ventilation system that pulled in external air, and only some passive heating from the side walls occurred. In contrast, each T+OTC had two complementary heating systems including an external 6 m-long plastic sleeve containing large black-painted stones from which heated air was pulled into the OTC by a fan and an external, 2000 W electric heater with its own air ventilation system. The air temperature inside each OTC was recorded every 15 min with a data logger (Cavadevices, Buenos Aires, Argentina) as was the ambient air temperature in the adjacent nursery. A controller system was used to shut off the electric heaters if the T+OTCs exceeded the + 4 °C target temperature above the Tc OTCs. The mean weekly temperatures of the T+OTCs were 3.9 and 3.2 °C higher than those of the Tc OTCs in 2018 and 2019; respectively (Fig. 1). Furthermore, the Tc OTCs were within 1 °C of the ambient temperature. Further design details of the OTCs can be found in Miserere et al. (2019b).
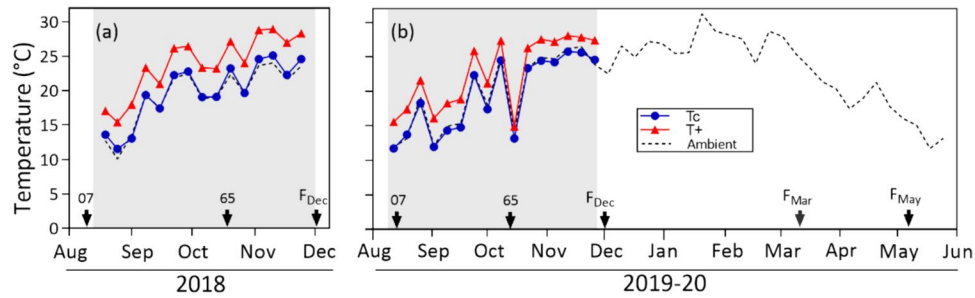
Fig. 1 Weekly mean daily air temperature (°C) in control (Tc) and warmed (T+) open top chambers (OTCs) and the ambient outdoor temperature during the 2018 (**a**) and 2019 experiments (**b**). Gray areas indicate the treatment periods. The symbols represent the average of 8 OTCs per temperature level. The approximate start of leaf growth (BBCH 07) and full bloom (BBCH 65) are indicated for well-irrigated, control trees. Fruit samples were taken in December 2018 the first season (F_{Dec}) when fruit number was very low and in December 2019, March 2020, and May 2020 the second season

Irrigation was applied using a pressurized drip irrigation system with a programmable electronic controller. The 100% irrigation trees received the equivalent of all the water that they consumed. To estimate this consumption, two pots from each of the 100 Tc and 100 T+ temperature levels were weighed on two consecutive days twice a week using a precision balance (Moretti, Model MPF, Buenos Aires, Argentina), and irrigation was performed every 3 days with two drip emitters (1.2 L h^{-1}) per pot to re-supply the consumption. The two-year-old, cv. Arbequina trees received 91 and 98 L of irrigation in 100 Tc and 100 T+; respectively, during the experimental period in 2018. In 2019, the irrigation was 160 L in 100 Tc and 204 L in 100 T+ in three-year-old cv. Coratina trees. The deficit irrigation combinations simply received 50% irrigation compared to 100 Tc or 100 T+ using one drip emitter (1.2 L h^{-1}) per pot. Aluminum foil-covered insulation was placed over the soil surface and drip emitters to reduce soil evaporation and exclude most precipitation. Soil relative extractable water (%) was most often above 80% in the well-watered, trees and near 60% in the deficit irrigation trees (Iglesias et al. 2023). The midday stem water potentials were −1.8 (100 Tc), −2.3 (100 T+), −2.1 (50 Tc), and −2.9 MPa (50 T+) at the end of the experimental period in cv. Arbequina (2018). The values were −2.7 (100 Tc), −3.4 (100 T+), −3.5 (50 Tc), and −4.0 MPa (50 T+) at the end of the experimental period in cv. Coratina (2019). More details are given in Iglesias et al. (2023).

Shoot elongation

Apical elongation (cm) of vegetative and reproductive shoots was evaluated as a measure of plant growth during the treatment period. The term vegetative shoot refers to young shoots with no inflorescences that were formed late in the previous growing season or at the start of the current season. Reproductive shoots were one-year-old shoots with inflorescences. Three young vegetative shoots per tree were randomly selected after the beginning of each season, and three reproductive shoots per tree were also added in the 2019 experiment when flowering was greater. In each case, the initial shoot length was measured with a ruler and the number of nodes with fully developed leaves were counted. Shoot length and number of nodes were then determined every two to three weeks during the treatments. Shoot elongation was calculated as the difference between the initial shoot length and length on a particular date.

Flowering and fruit set

Full bloom was considered to occur when at least 50% of the flowers were open (Sanz-Cortés et al. 2002). The date was not determined for each tree of cv. Arbequina in the various treatments in 2018 because very little flowering occurred, although the inflorescence number per tree (# tree^{-1}) was counted. The bloom date for cv. Coratina in 2019 was evaluated based on weekly observations during the treatment period of three, marked reproductive shoots per tree. Both inflorescence and leaf density (# m^{-3}) in cv. Coratina were determined by counting the number of inflorescences or leaves; respectively, inside a known cubic volume (0.2 m × 0.2 m × 0.2 m) in two canopy positions per tree. The number of inflorescences was also measured on the three marked, reproductive shoots. Fruit set was defined as the transformation of an ovary to a rapidly growing fruit after successful pollination and fertilization. Thus, fruit set calculations excluded small, seedless parthenocarpic fruit (i.e., shot berries). Fruit set (%) was estimated at the end of the experimental period in each cultivar by dividing normal fruit number by inflorescence number. The number of flowers per inflorescence was not counted for expressing fruit set (%) on a per flower basis.

Fruit size and weight

Fruit samples of 50 fruit tree^{-1} were taken when available in early December at the end of the experimental periods for both cv. Arbequina in 2018 and cv. Coratina in 2019. Additional samples were also taken later in the season in March and May 2020 for cv. Coratina to assess post-treatment responses to the previous irrigation deficit and warming. The fruit lengths and widths of the cv. Coratina samples were measured with a digital caliper, and the maturity index (MI) for these samples was determined visually by sorting the 50 fruit into eight classes (0 to 7) according to skin and pulp color (Uceda and Hermoso 2001). Fruit weight (g fruit^{-1}) was expressed on a dry basis after drying in an oven until a constant weight was reached. Dried material of cv. Coratina fruit was later ground for measuring fruit oil concentration (%) with nuclear magnetic resonance (NMR; model SLK200, Spinlock, Argentina). In some cv. Coratina trees, all fruit were harvested in March 2020 because an advanced maturity index (MI = 5; black skin with pulp turning purple) led to early fruit drop.

Vegetative biomass and fruit and oil yield

Vegetative biomass production (g tree^{-1}) and its partitioning into individual organs (leaves, branches, trunk, roots) was determined in one of the two trees per OTC at the end of the experimental period in December in 2018 and 2019. Biomass production was calculated as the difference between the initial biomass of three representative trees before the experiment and the biomass of each evaluated tree after the treatments. The below-to-above-ground biomass ratio was also calculated with fruit biomass being included in the above-ground biomass. Tree roots were carefully separated from the soil with a fine mesh sieve. The biomass of each organ was dried in an oven at 75 °C until constant weight.

Fruit yield (g tree^{-1}) on a dry weight basis was determined at the end of the experimental period in 2018 and 2019 in one tree per OTC. Additionally, a second tree per OTC was harvested later in March or May depending on maturity index in cv. Coratina (2019). Parthenocarpic fruit were separated from normal fruit when they occurred and their percentage relative to the total fruit number was calculated. The number of parthenocarpic or normal fruit per tree was determined by dividing the total weight of parthenocarpic or normal fruit by the dry weight of 50 fruit from either of these two categories. Oil yield (g tree^{-1}) was determined by multiplying fruit yield by oil concentration (%).

Statistical analyses

The effects of deficit irrigation, warming, and their interactions were determined for most variables using standard two-way analysis of variance (Agricolae package, R Core team, 2020). When statistically significant effects were detected, differences between treatment means were assessed using Tukey's tests (p < 0.05). Shoot elongation was evaluated using mixed models with irrigation, warming, and their interactions as fixed factors and date as a random factor (nlme package, R Core Team, 2020). All figures were created using Prism version 8 for Windows (GraphPad Prism Software, San Diego, USA).

Results

Shoot elongation

Vegetative shoot elongation was reduced by deficit irrigation at both temperature levels throughout the experimental period in cv. Arbequina in 2018 (p < 0.01; Fig. 2a). Warming
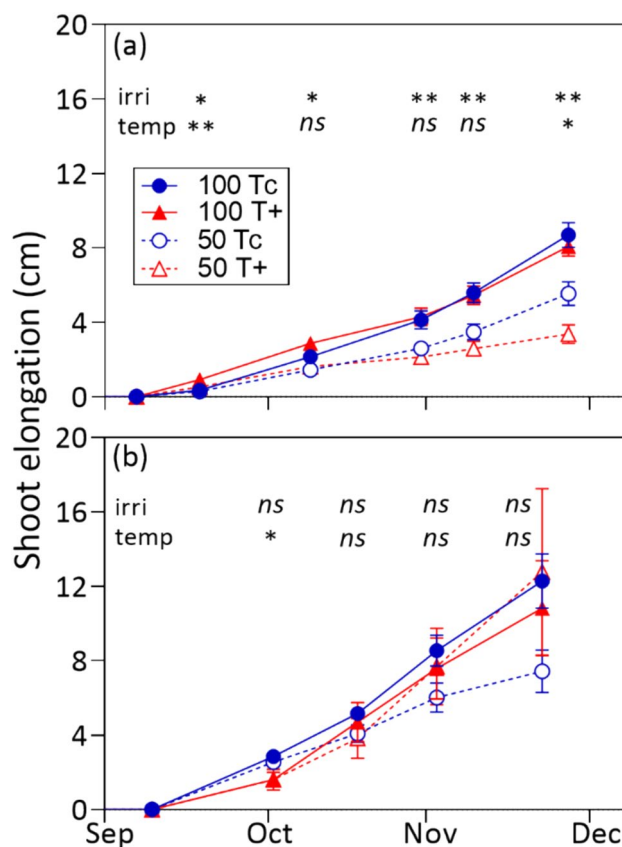

Fig. 2 Vegetative shoot elongation in the different irrigation (100%, 50%) and temperature (near-ambient control, Tc; warming treatment, T+) combinations in (**a**) two-year-old, cv. Arbequina trees in 2018 and (**b**) three-year-old, cv. Coratina trees in 2019. Each data point represents a mean ± SE (n = 4 OTCs). The statistical probability levels for irrigation and temperature are given as not significant (*ns*), p < 0.05 (*) , and p < 0.01 (**). No interactions were found between factors

increased shoot elongation very early in the season when air temperatures were low, but decreased elongation at the end of the treatments when temperatures were high (p < 0.05). In cv. Coratina in 2019, vegetative shoot elongation was not affected by deficit irrigation, and little response to temperature was observed (Fig. 2b). Similar results were obtained for the elongation of reproductive shoots (i.e., with fruit) in 2019 (data not shown).

Flowering and fruit set

Full bloom date of each treatment combination was not estimated in cv. Arbequina in 2018 due to the very low number of inflorescences. When measured in cv. Coratina in 2019, full bloom was 19–31 days earlier in T+ than in Tc (p < 0.01; Table 1). Furthermore, a significant irrigation x temperature interaction showed that full bloom was 9 days later under deficit irrigation at the control temperature, while no delay was observed under deficit irrigation with warming (T+).

The inflorescence density (# tree^{-1}) was greater in the well-irrigated control trees (100 Tc) than in the other treatment combinations in cv. Arbequina in 2018 (p < 0.05; Table 1). Additionally, warming reduced inflorescence density under well-irrigated conditions, but not under deficit irrigation. Inflorescence density (# m^{-3}) was about 15% lower in T+ than Tc under both irrigation levels in cv. Coratina in 2019, although a statistically significant difference was not detected (p = 0.08). Fruit set was decreased by T+ in cv. Arbequina during 2018 despite low inflorescence density, but a decrease was not apparent in cv. Coratina in 2019 (Table 1). Lastly, leaf density was lower in T+ than in Tc for cv. Coratina at the end of the experimental period (Table 1, p < 0.05).

Fruit number, size, and weight

Fruit number was greater under the well-irrigated control trees (100 Tc; 53 fruit tree^{-1}) than under the other treatment combinations (< 5 fruit tree^{-1}) at the end of the experimental period in cv. Arbequina in 2018 (p < 0.05). When excluding small parthenocarpic fruit, fruit number in cv. Coratina was much lower in T+ than in Tc trees at the end of the experimental period in 2019 and at final harvest (p < 0.05; Fig. 3) with no difference detected due to deficit irrigation. The percentage of parthenocarpic fruit tended to be greater in T+ than in Tc trees (p = 0.07; Fig. 4), which contributed to the decrease in normal, commercially viable fruit.

Table 1 Full bloom date (day of the year; DOY), inflorescence and leaf densities, and fruit set under the different combinations of irrigation (100%, 50%) and temperature (near-ambient control, Tc; warming treatment, T+) in two-year-old cv. Arbequina trees in 2018 and three-year-old cv. Coratina trees in 2019

Cultivar	Treatment		Full	Density		Fruit
	Irrigation	Temp	Bloom	Inflor	Leaf	set
			(DOY)	(# tree^{-1})	(# tree^{-1})	(%)
Arbequina	100	Tc	na	49 ± 18*c*	na	108 ± 62
	100	T+	na	0.4 ± 0.2*a*	na	63 ± 47
	50	Tc	na	5 ± 1*b*	na	79 ± 36
	50	T+	na	5 ± 2*b*	na	0
	irri			*		*ns*
	temp			*		*
	interaction			*		*ns*
			(DOY)	(# m^{-3})	(# m^{-3})	(%)
Coratina	100	Tc	284 ± 2*b*	3172 ± 324	5992 ± 472	48 ± 10
	100	T+	265 ± 2*a*	2688 ± 315	4867 ± 211	28 ± 10
	50	Tc	293 ± 2*c*	3375 ± 385	6336 ± 324	35 ± 6.3
	50	T+	262 ± 1*a*	2758 ± 128	5430 ± 473	26 ± 7.1
	irri		*ns*	*ns*	*ns*	*ns*
	temp		**	*ns*	*	*ns*
	interaction		**	*ns*	*ns*	*ns*

Each value represents a mean ± SE (n = 4 OTC)

na not available

The statistical probability levels for irrigation, temperature, and their interaction are given as not significant (*ns*), p < 0.05 (*), and p < 0.01 (**)

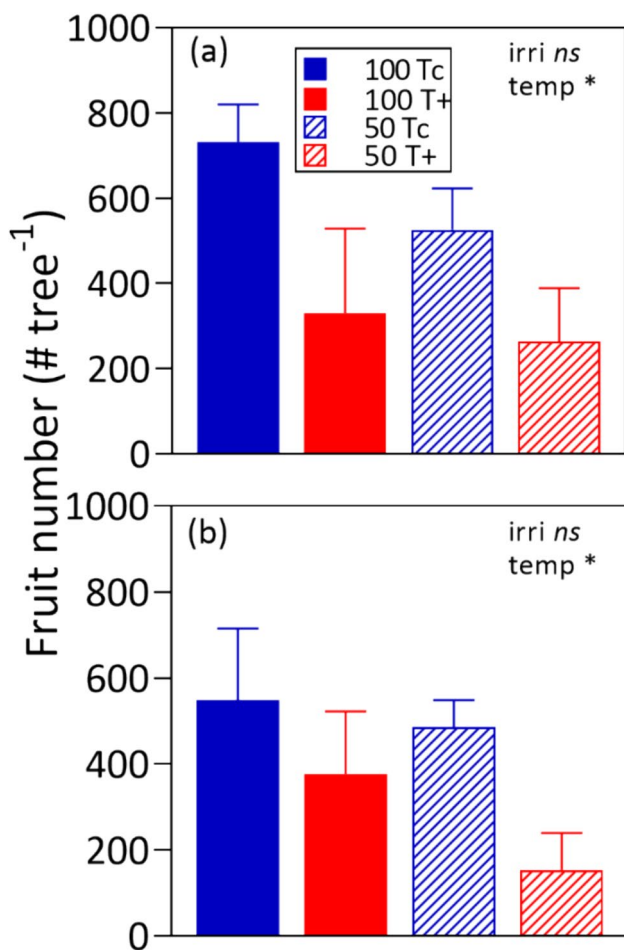Different italic letters are given when a significant interaction occurred

Fig. 3 Fruit number (# tree^{-1}) in the different irrigation (100%, 50%) and temperature (near-ambient control, Tc; warming treatment, T+) combinations in three-year-old, cv. Coratina trees after fruit set at (**a**) the end of the experimental period (December 2019) and (**b**) final harvest (March or May 2020). Each bar represents a mean ± SE (n = 4 OTCs). The statistical probability levels for irrigation and temperature are given as not significant (*ns*), p < 0.05 (*), and p < 0.01 (**). No interactions were found between factors. Parthenocarpic fruit were excluded from fruit number in this figure

Fig. 4 Parthenocarpic fruit (%) in the different irrigation (100%, 50%) and temperature (near-ambient control, Tc; warming treatment, T+) combinations in three-year-old, cv. Coratina trees in 2019. Each bar represents a mean ± SE (n = 4 OTCs). The statistical probability levels for irrigation and temperature are given as not significant (*ns*), p < 0.05 (*), and p < 0.01 (**). No interactions were found between factors

When measured in cv. Coratina, individual fruit weight was much higher in T+ than in Tc trees at the end of the experimental period (p < 0.01; Table 2). Although fruit length was not significantly different between T+ and Tc fruit, width was greater in T+ fruit. Additionally, the length/width ratio was lower in T+ fruit (p < 0.01). Deficit irrigation did not affect fruit weight or its dimensions at the end of the experimental period despite an average midday stem water potential during the spring of about −3.0 and −2.0 MPa in deficit- and well-irrigated trees; respectively. After three months without treatments (March), no significant differences in fruit weight or width were apparent due to warming. However, the length/width ratio was still statistic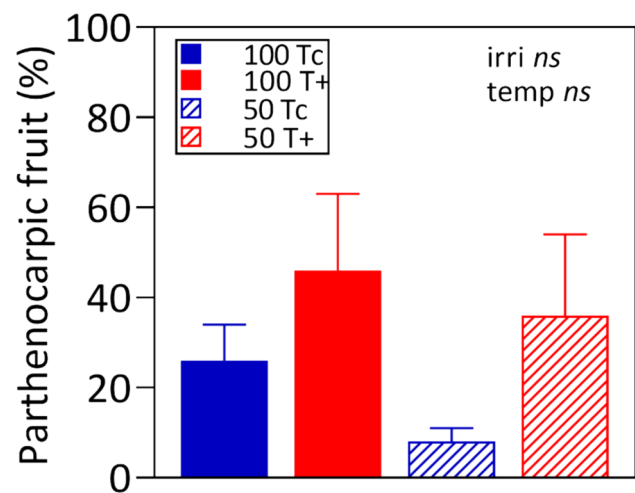ally lower in T+ fruits (p < 0.05). The fruit maturity index showed no treatment differences in March due to considerable variability among trees.

Vegetative biomass and yield

The total biomass production of all vegetative organs (g tree^{-1}) was lower in deficit-irrigated trees at the end of the experimental period in cv. Arbequina in 2018 (p < 0.01; Fig. 5a). This was largely due to less leaf biomass being produced under deficit irrigation (Table 3). In contrast, warming did not affect vegetative biomass. In cv. Coratina (2019), no differences in total vegetative biomass production or that of individual organs were apparent between temperature or irrigation levels (Fig. 5b; Table 3). Leaf biomass production values for cv. Coratina (i.e., the differences during the experiment between new leaf biomass and senesced leaf biomass) were low in all trees due to the senescence of older leaves during the spring in these three-year-old trees (Table 3).

Similar to fruit number, fruit biomass was greater under the well-irrigated control trees (100 Tc; 19.3 g tree^{-1}) than the other treatment combinations (< 2.0 g tree^{-1}) at the end of the experimental period in cv. Arbequina in 2018 (p < 0.05). In contrast, the fruit biomass in cv. Coratina did not show any significant differences between treatments at the end of the experimental period in December (Fig. 6a). This likely occurred because although fruit number was lower in the T+ than in the Tc trees (Fig. 3), earlier flowering in T+ trees contributed to greater individual fruit weight at the end of the experimental period (Tables 1, 2). Fruit yield at final harvest was indeed lower in the T+ trees when

Table 2 Fruit dry weight, dimensions, and maturity index under the different combinations of irrigation (100%, 50%) and temperature (near-ambient control, Tc; warming treatment, T+) in three-year-old cv. Coratina trees at the end of the experimental period (December 2019) and three months after the treatments (March 2020)

Date	Treatment		Weight (g)	Length (mm)	Width (mm)	Length/Width	Maturity index (0–7)
	Irrigation	Temp					
December	100	Tc	0.37 ± 0.03	17.6 ± 0.5	10.5 ± 0.2	1.68 ± 0.04	0
	100	T+	0.66 ± 0.09	18.5 ± 0.7	12.1 ± 0.7	1.54 ± 0.04	0
	50	Tc	0.34 ± 0.02	17.2 ± 0.3	10.3 ± 0.2	1.67 ± 0.02	0
	50	T+	0.64 ± 0.06	17.6 ± 0.5	11.8 ± 0.7	1.51 ± 0.05	0
	irri		*ns*	*ns*	*ns*	*ns*	*ns*
	temp		**	*ns*	**	**	*ns*
March	100	Tc	1.51 ± 0.31	21.5 ± 1.6	15.8 ± 1.1	1.36 ± 0.02	2.0 ± 0.8
	100	T+	1.59 ± 0.16	21.2 ± 1.0	16.5 ± 0.8	1.29 ± 0.02	2.7 ± 1.3
	50	Tc	1.39 ± 0.05	21.0 ± 0.9	15.6 ± 0.8	1.35 ± 0.03	0.5 ± 0.3
	50	T+	1.67 ± 0.09	22.0 ± 0.8	16.6 ± 0.8	1.33 ± 0.02	3.8 ± 1.3
	irri		*ns*	*ns*	*ns*	*ns*	*ns*
	temp		*ns*	*ns*	*ns*	*	*ns*

Each value represents a mean ± SE (n = 4 OTC)

The statistical probability levels for irrigation and temperature are given as not significant (*ns*), $p < 0.05$ (*), or $p < 0.01$ (**)

The p-values of the irrigation x temperature interaction were not significant

differences in individual fruit weight were no longer apparent (Fig. 6b; Table 2). Lastly, oil yield also tended to be lower in T+ than in Tc trees at final harvest (p = 0.07; Fig. 7) with oil concentrations (%) being about 42% in all treatment combinations.

Discussion

The responses of olive trees to combined irrigation deficit and warming are largely unknown. A companion study found that stomatal conductance and net photosynthesis were negatively affected by moderate irrigation deficit (50%) in many instances during the late winter and spring, but warming (+ 4 °C) either increased or decreased gas-exchange depending on whether the air temperatures were sub- or supra-optimal, respectively (Iglesias et al. 2023). In contrast, irrigation deficit and warming combined to additively reduce stem water potential throughout the late winter and spring. The present study indicates that aspects of reproductive development including full bloom date, flowering intensity and fruit set were sensitive to warming, which led to lower fruit numbers and yields at final harvest. Although moderate deficit irrigation had less effect on reproductive development, vegetative growth appeared to be negatively affected by deficit irrigation at least in cv. Arbequina when fruit load was low.

Shoot growth during the spring is important because it provides new nodes with lateral buds that produce inflorescences the next season. When shoot growth was still very

low in the late winter of 2018, deficit irrigation decreased the shoot elongation of young, two-year-old cv. Arbequina trees, while warming increased shoot elongation (Fig. 2a). Later in the spring under higher temperatures, deficit irrigation and warming combined to decrease shoot elongation. Such decreases due to deficit irrigation have been previously reported in many studies for the same time of year in more mature trees (Pierantozzi et al. 2014; Trentacoste et al. 2019). In three-year-old cv. Coratina trees in 2019, it should be noted that neither deficit irrigation nor warming reduced shoot elongation over the course of the experimental period (Fig. 2b). This likely occurred because deficit-irrigated, warmed trees (50 T+) had little fruit (Fig. 3), so additional photoassimilates would have been available for vegetative growth as has been found in fruit removal experiments (Dag et al. 2010; Fernández et al. 2015). At the regional level, it has been suggested that shoot growth will likely be greater in warm regions than colder ones (Gómez del Campo et al. 2010), but this may be more related to differences in growth season duration between locations than to warming during a certain period of time at the same location. The temperature above which shoot growth becomes inhibited should also be determined.

Full bloom date is known to change along latitudinal or altitudinal gradients and is of interest for estimating the risk of frost damage in a given region. When estimated in cv. Coratina in 2019, full bloom was 19 to 31 days earlier in T+ trees (+ 4 °C) than Tc trees (Table 1). Full bloom date measured in several cultivars along a latitudinal gradient in western Argentina was similarly observed to be 26 days
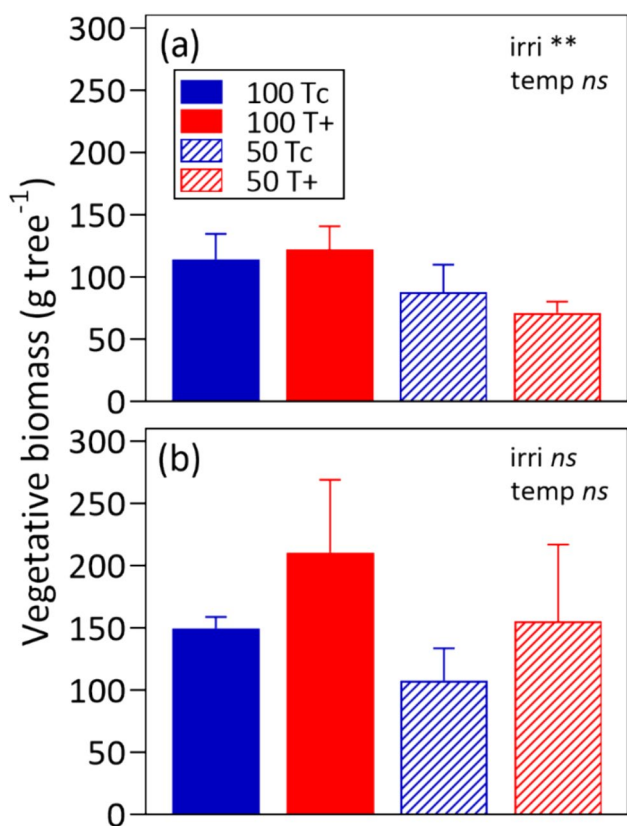
Fig. 5 Vegetative biomass production (g tree^{-1}) in the different irrigation (100%, 50%) and temperature (near-ambient control, Tc; warming treatment, T+) combinations in (**a**) two-year-old, cv. Arbequina trees in 2018 and (**b**) three-year-old, cv. Coratina trees in 2019. Each bar represents a mean ± SE (n = 4 OTCs). The statistical probability levels for irrigation and temperature are given as not significant (*ns*), p < 0.05 (*), and p < 0.01 (**). No interactions were found between factors

earlier at the warmest location with air temperatures differing by 5 °C along the gradient (Hamze et al. 2022). When considering the combined irrigation x temperature response in our study, full bloom was delayed by 9 days under deficit irrigation at the control temperature, while no significant delay was observed under deficit irrigation with warming. Under slightly cooler temperatures than occur at our location, moderate deficit irrigation (50% ETc) was found to delay flowering by 4 days (Pierantozzi et al. 2014). This information suggests that water deficit will have less impact than warming on full bloom date. However, the combined irrigation x temperature response found in the present study may not be easily predicted from single factor studies. Further multiple-factor studies in a wide range of cultivars and locations are needed.

Flowering intensity and fruit set are key yield determinants in olive trees and often vary between years due to climate and other factors (Lavee 1996; Rosati et al. 2023). Although flowering density was very low in two-year-old cv. Arbequina trees in 2018, inflorescence number was greater in the well-irrigated control trees at near-ambient temperature (100 Tc) than in the warming or deficit irrigation treatment combinations (Table 1). The decrease in flowering intensity under the warming treatment appeared to occur even though cv. Arbequina fulfilled its chilling requirements in our region in 2018 prior to the start of the experimental warming (Hamze et al. 2022). The number of chilling units were calculated to be 931, while only 339 are reported to be required for cv. Arbequina (De Melo-Abreu et al. 2004; Aybar et al. 2015). It has been suggested that once sufficient chilling has been accumulated, later temperatures of about 30º C can inhibit reproductive bud break

Table 3 Vegetative organ biomass production and below-to-above-ground biomass ratio under the different combinations of irrigation (100%, 50%) and temperature (near-ambient control, Tc; warming treatment, T+) in two-year-old cv. Arbequina trees in 2018 and three-year-old cv. Coratina trees in 2019

Cultivar	Treatment		Organ biomass (g)				Below/above
	Irrigation	Temp	Root	Trunk	Branch	Leaf	
Arbequina	100	Tc	16 ± 7	15 ± 1	36 ± 6	48 ± 8	0.43 ± 0.01
	100	T+	25 ± 10	10 ± 1	38 ± 6	48 ± 6	0.49 ± 0.03
	50	Tc	20 ± 14	10 ± 2	29 ± 7	29 ± 10	0.52 ± 0.08
	50	T+	15 ± 7	11 ± 1	23 ± 4	22 ± 6	0.47 ± 0.10
	irri		*ns*	*ns*	*ns*	*	*ns*
	temp		*ns*	*ns*	*ns*	*ns*	*ns*
Coratina	100	Tc	45 ± 12	40 ± 7	65 ± 6	0 ± 3	0.35 ± 0.01
	100	T+	61 ± 31	33 ± 10	106 ± 44	11 ± 11	0.39 ± 0.03
	50	Tc	28 ± 17	24 ± 7	64 ± 13	9 ± 4	0.37 ± 0.03
	50	T+	35 ± 19	35 ± 9	91 ± 21	5 ± 16	0.38 ± 0.03
	irri		*ns*	*ns*	*ns*	*ns*	*ns*
	temp		*ns*	*ns*	*ns*	*ns*	*ns*

Each value represents a mean ± SE (n = 4 OTC)

The statistical probability levels for irrigation and temperature are given as not significant (*ns*), p < 0.05 (*), and p < 0.01 (**)

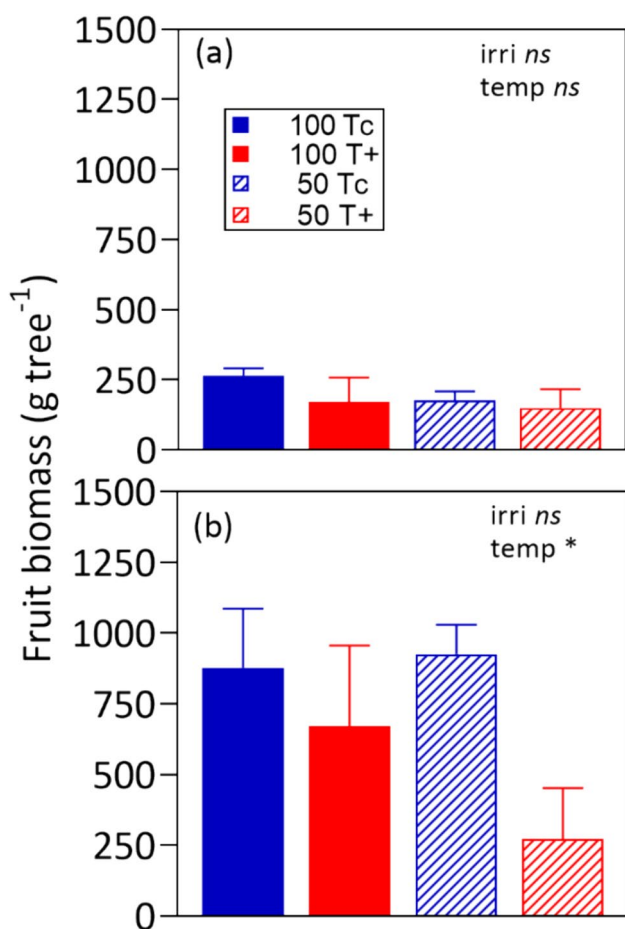The p-values of the irrigation x temperature interaction were not significant

Fig. 6 Fruit biomass in the different irrigation (100%, 50%) and temperature (near-ambient control, Tc; warming treatment, T+) combinations in three-year-old, cv. Coratina trees at (**a**) the end of the experimental period in December 2019 and (**b**) final harvest (March or May 2020). Each bar represents a mean ± SE (n = 4 OTCs). The statistical probability levels for irrigation and temperature are given as not significant (*ns*), $p < 0.05$ (*), and $p < 0.01$ (**). No interactions were found between factors
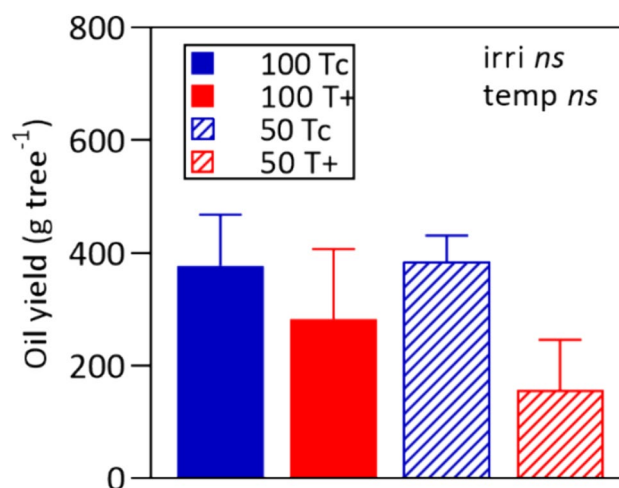

Fig. 7 Oil yield in the different irrigation (100%, 50%) and temperature (near-ambient control, Tc; warming treatment, T+) combinations in three-year-old, cv. Coratina trees. Each bar represents a mean ± SE (n = 4 OTCs). The statistical probability levels for irrigation and temperature are given as not significant (*ns*), $p < 0.05$ (*), and $p < 0.01$(**). No interactions were found between factors

(Rubio-Valdés et al. 2022). Under our experimental conditions, midday temperatures were most often above 30 °C by late winter (mid-August) in the T+OTCs, but not in the control chambers (Iglesias et al. 2023). It should be noted that the flowering response to warming in our study primarily occurred in the well-watered trees with warming not causing additional decreases in flowering intensity under deficit irrigation. Similar to the results in cv. Arbequina, deficit irrigation during early inflorescence formation has been shown to reduce inflorescence numbers in young, potted cv. Picual trees (Rapoport et al. 2012). In three-year-old cv. Coratina with moderate to high flowering in 2019, inflorescence number was about 15% lower in T+ than Tc trees under both irrigation levels, but a statistically significant difference was not apparent (p = 0.08; Table 1). The number of chilling units accumulated in 2019 (1200) was somewhat

higher than in 2018 (931). It is likely that some combination of cultivar response, climate conditions, and the young age of the trees explains the different responses of flowering intensity in the 2018 and 2019 experiments. Similar to inflorescence number, fruit set (%) was significantly reduced by warming in 2018 in cv. Arbequina, but not in 2019 in cv. Coratina. In another experimental warming study, although inflorescence number was not decreased in cv. Picual with warming (+ 4 °C) over three years, a decrease in fruit set (%) was observed (Benlloch-González et al. 2018). In that case, the winter temperatures associated with the warming treatment presumably allowed for chilling requirements to be met under the Mediterranean climate conditions, but fruit set in cv. Picual appeared to be sensitive to high temperature (30 °C) and its accompanying low humidity likely due to reduced pollen germination or subsequent pollen tube growth (Cuevas et al. 1994; Koubouris et al. 2009; Vuletin Selak et al. 2013). Additionally, although irrigation deficit was not evaluated by the authors (Benlloch-González et al. 2018), they suggested that the irrigation season should start earlier in the Mediterranean under increasing temperatures with global warming to avoid water deficit during inflorescence formation and full bloom.

Fruit number and individual fruit weight may both be sensitive to deficit irrigation and warming in the late winter and early spring. Due to less flowering intensity and fruit set under deficit irrigation and warming, fruit number was greater in the well-irrigated control trees than the other treatment combinations at the end of the experimental period in cv. Arbequina in 2018. Fruit number in cv. Coratina was also much lower in T+ than in Tc trees when excluding small

parthenocarpic fruit, but no difference was detected due to deficit irrigation (Figs. 3, 4). The substantial presence of parthenocarpic fruit with warming in our study experimentally confirms the suggestion by other authors that parthenocarpic fruit are more common at least in some cultivars under high temperatures (Cuevas et al. 1994), and it has been found that supplemental pollen application could reduce this phenomenon in hot environments (Ayerza and Coates 2004). Although fruit number per tree was not reported by Benlloch-González et al. (2018), fruit number on bearing branches was much lower in all three years of warming (+ 4 °C) in cv. Picual due to lower fruit set. When measured in cv. Coratina in our study, individual fruit weight was much higher in T+ than in Tc trees at the end of the experimental period, but deficit irrigation did not affect individual fruit weight (Table 2). The greater individual fruit weight at the end of the experimental period due to warming likely occurred because earlier flowering in T+ trees allowed for 3 to 4 weeks more of fruit growth at that point (Tables 1, 2). Additionally, there were fewer fruit in the T+ trees, which would have resulted in more photoassimilate availability per fruit given that net leaf photosynthesis was not negatively affected by warming except towards the end of the experimental period (Iglesias et al. 2023). By final harvest after several months without warming, the fruit development in the near-ambient temperature, control trees presumably caught up to that of the T+ fruit, and differences in individual fruit weight were no longer apparent. In a similar manner, fruit development appeared to show no further differences 45 days after experimental shading of large olive trees (Rousseaux et al. 2020). With respect to deficit irrigation, fruit growth may often not be reduced by moderate water stress in olive trees because of osmotic adjustments that maintain fruit turgor pressure (Girón et al. 2015).

The responses of vegetative biomass production and fruit yields to deficit irrigation and warming are potentially a function of several processes ranging from changes in stem water potential and net leaf photosynthesis to specific effects on yield determinants and components such as fruit number (Villalobos et al. 2023). When flowering and fruit number were generally low in cv. Arbequina in 2018 and water stress was moderate under deficit irrigation (i.e., midday stem water potential of −2.5 MPa towards the end of the experimental period), total vegetative biomass per tree decreased by 31% under deficit irrigation mostly due to less leaf biomass (Fig. 5, Table 3). This lower leaf biomass coincides with the lower shoot elongation (Fig. 2) reported here and the lower leaf photosynthesis shown in Iglesias et al. (2023). A similar study with young, potted cv. Cornicabra trees grown outdoors also reported a 30% reduction in total vegetative biomass production with a moderate 50% water deficit (Gómez-del-Campo et al. 2007). In contrast, no effect on vegetative biomass due to warming in cv. Arbequina was

observed even though shoot growth was slightly reduced by warming at the end of the experimental period. In 2019, the vegetative growth of cv. Coratina was not statistically different under deficit irrigation despite midday stem water potentials of −3.7 MPa in the deficit-irrigated trees towards the end of the experiment. Nevertheless, the vegetative biomass under deficit irrigation was 27% less on a percentage basis under deficit irrigation. It is likely that no significant difference was apparent in part due to variability in biomass production between trees. Additionally, the very low fruit number in the 50 T+ trees (Fig. 3) likely allowed for more photoassimilates to be available for vegetative growth in these trees. As was the case for cv. Arbequina, warming did not affect vegetative biomass in cv. Coratina. The three-year warming study in cv. Picual in southern Spain actually found greater pruning weight in the warming treatment each year, which was attributed to less fruit biomass per tree (Benlloch-González et al. 2019), and warming during oil accumulation after final fruit set in cvs. Arbequina and Coratina also increased glucose equivalent allocation to vegetative growth due to smaller fruit and lower oil concentrations (Miserere et al. 2022). The lower fruit yields in cvs. Arbequina and Coratina in our study at final harvest due to late winter and spring warming were mostly a function of lower fruit number in accordance with Benlloch-González et al. (2019).

Conclusions

Although results from young olive trees must be extrapolated with care, the responses reported here provide a first experimental approximation for predicting the consequences of deficit irrigation and global warming during the late winter and spring. Vegetative growth appeared to be more sensitive to moderate deficit irrigation than to experimental warming (+ 4 °C). However, yield determinants including flowering intensity and fruit set were more negatively affected by warming, which led to fewer fruit and less yield per tree. When determined in cv. Coratina, full bloom date was also much earlier due to warming, while deficit irrigation delayed flowering to a lesser degree. From a production perspective, it does not appear that many warming effects on reproductive development can be easily counteracted by adjusting irrigation amounts. Further studies with more mature trees and cultivars over several growing seasons are recommended to better assess the combined responses of deficit irrigation and warming. This would provide needed information on potential carry-over effects such as how decreased fruit number due to warming the first season would affect yield in subsequent seasons.

Declarations

Conflict of interest The authors declare no conflicts of interest related to this article.

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