Environmental Stresses and Sustainable Olive Growing

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Abstract

The olive tree, *Olea europaea* L. is resistant to soil water deficit, high irradiance, high temperature and high vapour pressure deficit. Olive trees are also more resistant to salinity than most perennial crops, but sensitive to low oxygen conditions in the soil and low temperature. Traditional orchard management already takes advantage of adaptive features of the species to the environment, but environmental issues and the expansion of olive growing to new areas where climates and soils are often not optimal require revisiting criteria for orchard design and management protocols. The mechanisms of adaptation of olive trees to main environmental stresses (drought, salinity, temperature) are here reviewed as well as the implications of olive stress physiology on sustainable management of olive growing.

INTRODUCTION

Sustainable agriculture is a widely used, and sometimes abused, term in current literature and common language, although its origin is relatively recent. The concept of sustainable agriculture was developed in the early 1980s based on principles of stability and ecological interaction. Among the many definitions reflecting different points of view, the following framework definition "an agriculture that can evolve indefinitely towards greater human utility, greater efficiency of resource use, and a balance with the environment that is favourable both to humans and to most other species" (Harwood, 1990) emphasizes the relationship between the crop response and the efficient use of resources and/or interaction with environmental factors.

Suboptimal performance in growth and productivity of crops is often caused by limiting environmental conditions. On the other hand, there are cases when deviations from non-stressful conditions may be beneficial. For instance, exposure of olive plants to abiotic stress may improve fruit quality (Gucci et al., 2009), oil quality (Servili et al., 2007) and induce physiological adjustments that protect the tissues from subsequent adverse responses that would occur if such stress were abruptly imposed (Tattini et al., 1995). Olive trees are resistant to drought, high temperatures, and high irradiance, and more tolerant to salinity than other fruit trees. On the other hand, olive trees are sensitive to low temperature and waterlogging, conditions that limit the geographical distribution of this species to areas with Mediterranean climate, characterized by dry summers, mild winters, and precipitations concentrated in autumn and spring but variable from year to year.

The main mechanisms of adaptation of olive trees to major environmental stresses (drought, salinity, temperature) are briefly illustrated here as well as the implications for orchard productivity and sustainability.

RESPONSES TO ENVIRONMENTAL STRESS

Drought

Olive trees are very resistant to water scarcity in the soil. Physiological mechanisms of adaptation of olive plants to soil water deficit include stomatal closure, the decrease of leaf water potential (ψ_w), osmotic adjustment, maintenance of cellular turgor at low values of relative water content (RWC), maintenance of a high water potential gradient between the canopy and the root, and low probability of cavitative events in the xylem (Lo Gullo and Salleo, 1988; Salleo and Nardini, 1999).

Stomatal closure effectively decreases transpiration rate and water loss. The stomatal response to decreasing humidity in the soil is initially slow compared with more responsive species like apricot or kiwifruit, and stomata remain relatively open even at low leaf ψ_w. Photosynthesis also remains active at low ψ_w. At pre-dawn ψ_w of -4 MPa photosynthetic rates (A) of 6.5 µmol m^{-2} s^{-1} have been measured and A was still 10% of that of fully-irrigated, potted plants at -6 MPa (Angelopoulos et al., 1996). In field-grown trees subjected to various irrigation regimes A reached 50 and 25% of maximum values at pre-dawn ψ_w of about -1.75 and -4.5 MPa, respectively (Caruso, 2010), confirming the high tolerance of the photosynthetic apparatus to water deficit. During initial or intermediate stages of water deficit, the inhibition of photosynthesis is mainly due to the decrease of stomatal conductance, whereas the damage to photosystem II is minor (Centritto et al., 2005).

The turgor loss point for the olive leaf has been estimated to occur at -3.0-3.5 MPa ψ_w, equivalent to 75-80% RWC (Lo Gullo and Salleo, 1988). On a diurnal basis the ψ_w decreases due to the loss of water, the high stem hydraulic resistances and the rigidity of cell walls and reaches a minimum at midday. As a result, ψ_w approaches the turgor loss point during the hottest part of a summer day even when the substrate is moist. Leaf ψ_w as low as -8 MPa can be measured under extreme drought conditions, but olive trees retain the capacity to rehydrate and recover upon watering.

The anatomy of the xylem vessels is responsible for the relatively low hydraulic conductance and low occurrence of cavitation events. Almost 90% of the vessels in nodes and internodes of one-year-old shoots have a diameter less than 20 µm (Lo Gullo and Salleo, 1990). The narrow size of xylem vessels reduces the probability of embolism occurrence and blockage of the xylem pathway due to the formation of air bubbles as the water decreases in the soil and the water potential drops. At leaf ψ_w approximately corresponding to the cell turgor loss point, only about 5% of xylem vessels are disrupted because of embolism and stem hydraulic conductivity is reduced by 25-30% (Salleo and Nardini, 1999). The high safety of the hydraulic system against cavitation events during drought periods is counterbalanced by the low efficiency in sap flow since the flux is directly proportional to the fourth power of the radius of individual vessel elements according to the Poiseuille's Law.

Osmotic adjustment entails the synthesis and accumulation of osmotically active solutes that are metabolically compatible. The consequent decrease in ψ_w induced by the decrease in osmotic potential (ψ_π) allows the tissues to compensate for the effects of stress on turgor pressure. The extent of active osmotic adjustment in olive leaves when water is scarce is high, up to 1.5 MPa, and it is mainly due to the accumulation of sugar alcohols, soluble carbohydrates, organic acids, and proline (Gucci et al., unpublished results; Sofo et al., 2004). Both osmotic adjustment and the decrease in ψ_w increase the gradient between the root and the canopy, making water uptake possible at very low soil ψ_w values.

At the whole plant level, water deficits increase the root/shoot ratio, water use efficiency, radiation use efficiency, and modify root anatomy and physiology. The effects of water deficit on reproductive processes are often overlooked although they have a direct impact on yield. Olive fruit growth reportedly follows a double sigmoid type (Hartmann, 1949), but this pattern is probably the result of water limitations since it is not apparent in well watered trees (Gucci et al., 2009). Since endocarp expansion is usually over by 12 weeks after full bloom, water applied afterwards only stimulates mesocarp growth. A practical implication is that full irrigation is not absolutely necessary to achieve maximum mesocarp-to-endocarp ratio, an important quality feature for olive fruits both for table consumption and oil production. While it is well documented that irrigation increases the mesocarp-to-endocarp ratio when compared with rainfed trees (Gucci et al., 2009; Gomez-Rico et al., 2007; Lavee et al., 2007), recent work showed that some degree of water deficit increases or maintains the ratio similar to that of well irrigated trees

(Gucci et al., 2009). These findings allow the reconciliation of apparent contradictory reports on the effect of irrigation on pulp-to-pit ratio that likely depended on the degree and timing of the stress treatments that were compared with the fully irrigated controls (Table 1).

The yield response curve to evapotranspiration is non-linear, which means that at low crop water evapotranspiration (e.g., 450-550 mm crop evapotranspiration) the water required by the olive tree is about one third less of the water needed at 750-850 mm crop evapotranspiration (Moriana et al., 2003). Therefore, the water use efficiency (yield per unit of water per year) decreases as crop evapotranspiration increases beyond a certain level. If we express the fruit yield on a relative scale versus percent of water applied by irrigation during the fruit development period using data from several independent studies published in the last 10 years, we find a similar relationship in the initial part of the curve, then diminishing returns at high volumes of water applied (Fig. 1). When 50% of the full requirement of water is supplied to the trees the fruit yield is about 80% of the fully irrigated control. An essentially similar relationship is obtained if oil yield is plotted against percentage of full irrigation (Fig. 2). In both graphs the scatter of yield data points for rainfed or almost rainfed treatments is due to the different soil and climatic conditions of the respective studies (Figs. 1 and 2).

Deficit irrigation, that is applying less water than that needed by the tree, is to be recommended for sustainable olive growing. Deficit irrigation allows considerable savings of water while maintaining high yields and even increasing the phenolic concentration of the oil compared with fully-irrigated trees (Servili et al., 2007). Different strategies of deficit irrigation have been proposed and tested for olive growing. The deficit can be either distributed evenly throughout the irrigation season, or concentrated from pit hardening until the end of the summer, or imposed and relieved by short cycles during the irrigation period. All the above strategies appear equally effective and their choice should be based on rainfall pattern, soil texture and soil water storage capacity (Gucci et al., 2007; Moriana et al., 2003). On the other hand, partial root drying irrigation (Fernandez et al., 2006) or irrigating with different volumes depending on the tree crop load (full irrigation in “on” years, rainfed in “off” years, Moriana et al., 2003) are technically worse or economically less convenient than deficit irrigation strategies using the same amount of water.

Salinity

Soil salinity is one of the main factors limiting crop productivity in areas where plants are irrigated with saline water and exposed to high temperature and drought. Under these climatic conditions salts tend to accumulate in the soil because of the high evaporative demand and insufficient leaching of ions, problems often exacerbated by the presence of shallow saline-water table or use of brackish water for irrigation. Sodium chloride is usually the most common salt, but irrigation waters containing sodium bicarbonate or calcium sulphate are quite frequent too. Toxic effects for plants are mainly caused by excessive concentrations of Na^+, Ca^{2+}, Cl^-, and SO_4^{2-}.

Olive is considered a moderately salt tolerant crop, more tolerant than other temperate zone fruit trees (Gucci and Tattini, 1997). Concentration limits for growth and productivity have not been clearly identified as they vary according to the physiological process involved, environmental conditions, and cultivar. It has been reported that water containing from 2 to 4 g L^{-1} salt residue can be used to irrigate olive plants without major effects on survival, growth, yield or oil quality (Gucci and Tattini, 1997). On the other hand, growth is affected when plants are irrigated with water between 40 and 100 mM NaCl (Therios and Misopolinos, 1988; Benlloch et al., 1991). The onset of yield decline has been indicated to occur at 2.7 dS m^{-1} EC and a 10% reduction in yield at soil solution electrical conductivity between 4 and 6 dS m^{-1}. The maximum salt residue in irrigation water tolerated by olive trees has been estimated at a concentration of 8 g L^{-1} (Gucci and Tattini, 1997). Although these thresholds are quite generous, long-term performance of the olive orchard may be impaired by salts even if present in irrigation water at concentrations compatible with growth and productivity. In fact, in perennial crops salts progressively accumulate in the root zone and eventually become excessive and harmful. Under these conditions trees are apparently healthy in the first few years after orchard establishment, and then suddenly they develop symptoms and collapse. In order to alleviate these problems salts should be adequately leached by supplying excessive volumes of water to wash away toxic ions below the horizon explored by root systems.

Besides salt concentration, other factors affecting the salt tolerance of olive plants include genotype, plant age, duration and graduality of exposure, type of organ, soil and environmental conditions (Greenway and Munns, 1980; Gucci and Tattini, 1997). For instance, young plants or organs are more susceptible than mature ones; sudden salinization is more harmful than gradual exposure. Soil salinity changes plant morphology by decreasing leaf area, internode length, the number of shoots and leaves, and the canopy-root ratio of olive trees. Typical symptoms are chlorosis and/or necrosis of the apical part of young leaves that then extends to the whole lamina and to older leaves. Defoliation is an extreme mechanism whereby olive plants reduce their leaf area and the overall load of toxic ions. Visual symptoms appear when orchard performance has already been reduced and so they are virtually useless for management decisions. Moreover, visual assessment of salinity problems is unreliable since it is strongly dependent on soil and climate conditions and inadequate for detecting genotypic differences in most cases.

Salt tolerance in olive plants mainly depends on exclusion mechanisms that limit uptake and transport of Na^+ and Cl^- from the root to the canopy. This ability to regulate salt entry into the shoot can be used to screen genotypes for salt tolerance (Gucci and Tattini, 1997). An increase in K^+ selectivity partially compensates for the adverse effects of excess Na^+ on K^+ uptake and partitioning. The exclusion capacity tends to be saturated as stress is prolonged or NaCl concentration increased. Active osmotic adjustment contributes to maintain leaf turgor when the leaf ψ_w drops and it is mainly accomplished by inorganic solutes, soluble carbohydrates and sugar alcohols (Gucci et al., 1997), but cultivar differences in sensitivity are not related to inherent capacity to accumulate mannitol or other soluble carbohydrates (Tattini et al., 1996). Other factors conferring salt tolerance include the capacity to tolerate leaf dehydration and drastic reductions in leaf ψ_w, and the high hydraulic resistance in the stem (see also paragraph on drought), that allow the olive plant to maintain a large gradient in ψ_w between the root and the canopy. Salt-induced stomatal closure reduces transpiration and, thereafter, uptake and transport of Na^+ and Cl^- through the transpiration stream (Chartzoulakis et al., 2002; Therios and Misopolinos, 1988). Finally, adaptation to saline conditions can occur only if plants are able to meet the increased energy demand due to ion exclusion and compartmentation, biosynthesis of compatible solutes, and osmoregulation (all energy-requiring processes), while facing reductions in carbon assimilation (Gucci et al., 1998).

Resistant cultivars show a higher exclusion capacity for toxic ions than sensitive genotypes. Sensitive cultivars tend to accumulate Na^+ and Cl^- and they reach toxic concentrations of these ions earlier than tolerant cultivars. However, sensitive and tolerant cultivars often behave in a similar manner at low salt concentrations or during the initial stages of stress. A list of cultivars which have been extensively tested for salinity tolerance is given in Table 2.

From the applied point of view, cultivar choice at planting is the most effective horticultural tool for growing olive trees in areas affected by salinity (Table 2). There are many resistant cultivars available and more can be obtained with further research on genotype selection and breeding. Breeding should also be aimed at developing new rootstocks resistant to salinity, that are not yet available for olive growing. Second, growing olive trees under saline conditions requires proper management of water. The calculated leaching requirement must be fully satisfied so that tree roots can be maintained at a salt concentration similar or close to that of the irrigation water and within the limits tolerated by the species. Deficit irrigation practices should be used with caution and only if compatible with leaching requirements. Drainage can be useful to alleviate the problem of a high water table or to eliminate salts leached by rainfall or irrigation.

Fertilizers containing potentially toxic ions such as Na^+ and Cl^- should be avoided. Nevertheless, fertilization is indispensable to supply elements like K^+ and Mg^{2+} that are less absorbed when saline waters are used.

Temperature

Limitations in metabolism and productivity due to suboptimal temperatures are not unusual in areas where olive trees are cultivated. Reproductive processes, and flowering in particular, are affected by both low and high temperatures. Low temperatures and those above 30°C reduce pollination and fruit set, and favour embryo abortion. Irrigation can alleviate the effect of high temperatures by maintaining transpiration high and the gap between air temperature and that of transpiring organs wide.

Low temperatures inhibit the expansion of olive growing to northern latitudes or high altitudes. Chilling temperatures between 0 and 10°C are not lethal for the tree, but they can damage flower buds, flowers, and fruits. It has been shown that metabolic activity is drastically decreased below 10°C and maintenance of the cell membrane potential is impaired at temperatures between 7.5 and 12.5°C depending on the cultivar (Mancuso, 2000). Chilling temperatures also affect the water relations of the olive tree. Symptoms of fruit dehydration may develop in autumn and winter, even when the soil is moist due to an unbalance between water uptake and transpiration. These symptoms are more evident in high cropping years or when environmental conditions (high solar irradiance, mild air temperature and low soil temperature) favour high water demand and low uptake (Moriana, 2001). The physiological explanation is that at temperatures between 6.4 and 10°C the xylem and leaf ψ_w decrease and water uptake stops, whereas g_s decreases below 6.4°C soil temperature (Pavel and Fereres, 1998). As a result, in the interval between 6.4 and 10°C water uptake is inhibited but the foliage continues to transpire, albeit at a reduced rate, thanks to the water supplied from other organs and tissues. Wilting symptoms are more evident in fruits at an advanced stage of ripening than in immature fruits. A reduction in assimilation when temperature is below 5°C is in part attributed to plant dehydration but, when conditions favouring photoinhibition prevail the effect on dehydration becomes negligible (Bongi and Long, 1987).

Freezing temperatures affect tree physiology differently from chilling temperatures. As the temperature drops below 0°C extracellular ice formation is followed by the release of water from the inside of the cell due to the difference in vapour pressure between the apoplast and the symplast. This mechanism increases the concentration of the cell solution, decreases the ψ_π, and lowers the freezing point (Levitt, 1980). If the temperature continues to decrease, intracellular ice forms determining membrane disruption, ion leakage, loss of cellular compartmentalization, and finally cell death (Levitt, 1980). In olive trees lethal temperatures occur between -7 and -18°C, depending on the organ, cultural conditions and cultivar. There are cultivar differences in resistance, although only a few have been properly tested (Mancuso, 2000). Branches are more resistant than current-year shoots, leaves or annual organs like flowers and fruits. Prevailing environmental conditions can determine wide differences in resistance because acclimation is mainly triggered by the gradual decrease in temperature occurring in autumn and winter (Levitt, 1980). In contrast, the effect of photoperiod on acclimation is less clear in olive trees. In spring increasing temperatures determine loss of acclimation and tissues become more vulnerable to low temperature stress. From the practical point of view increased freezing resistance can be obtained by selecting the right site, resistant cultivars and favouring acclimation by avoiding irrigation, nitrogen fertilization or pruning in autumn.

CONCLUSIONS

Crop performance is often the result of interactions between multiple stresses and, therefore, it is not entirely predictable from responses to individual stresses. In areas where olive trees are grown concomitant occurrence of stresses is frequent. Salinity or droughts are often present in summer, when trees are also exposed to high temperature and high irradiance for most of the day. In winter low temperature stress is often associated with low oxygen in heavy soils with poor water drainage. Nutrient uptake does not only depend on soil nutrient concentrations, but also on available soil moisture. For example, leaf nitrogen concentration appears positively correlated with the amount of applied water since nitrogen uptake depends or soil water availability (Gucci et al., 2010). Salinity often determines nutrient deficiencies because of antagonistic effects in uptake and transport. The fruiting condition of the tree (high or low crop load) can markedly influence the tree response to environmental stresses or its input requirements (Fernandez-Escobar et al., 2000; Gucci et al., 2007).

Olive trees are less demanding in terms of water, nutrients and, generally speaking, energy inputs than other fruit trees. In this respect, sustainable cultivation can be achieved with few adjustments in management practices. For instance, if deficit irrigation strategies are adopted olive orchards require relatively low volumes of water annually. Deficit irrigation saves water and energy compared with full irrigation, increases water use efficiency, maintains adequate levels of leaf nitrogen and, hence, has a low environmental impact (Gucci et al., 2010; Moriana et al., 2003). Moreover, deficit irrigation is sustainable in the long run, it can be applied to young orchards and it allows producing high yields while optimizing the analytical and sensory profiles of the oil (Caruso, 2010; Gomez-Rico et al., 2007; Servili et al., 2007). Recent findings have also shown that it is possible to identify an optimal range of water supply for maximum yield and best quality of fruits and oils (Gucci et al., 2007, 2009; Servili et al., 2007).

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Tables

Table 1. A summary of irrigation effects on pulp-to-pit ratio of olive fruits from the literature. Symbols (+, -, =) indicate increase, decrease or equality respectively of high volumes of irrigation compared with low volumes (usually deficit irrigation or rainfed cultivation). Legend: ET_e, effective evapotranspiration; vs., versus.

Cultivar	Effect	Irrigation treatment	Author
Ascolana Tenera	= +	0, 33, 66, 100% ET_e	Patumi et al., 1999
Kalamata	= +	“	“
Nocellara Belice	= +	“	“
Itrana	+	“	d’Andria et al., 2004
Maiatica	+	“	“
Carolea	+	80 mm water (4 irrigations)	Inglese et al., 1996
Souri	=	1 to 3 irrigations	Lavee et al., 1990
Muhasan	+ = -	Various irrigation regimes	Lavee et al., 2007
Nocellara Belice	+ in 1980	1 to 3 irrigations	Baratta et al., 1986
“	= in 1981	“	“
Olia Manna	-	100 vs. 66 or 33% ET_e	Milella and Dettori, 1987
Arbequina	= in 1996/97	RDI 50 or 25% vs. 100% or RDI 75%	Alegre, 2001
“	+ in 1998	RDI 50 or 25% vs. 100% or RDI 75%	“
Cornicabra	=	Deficit vs. 100%	Gomez-Rico et al., 2007
“	-	125% vs. 100%	“
Frantoio	=	50 vs.100%	Caruso, 2010
	+	100 vs. 5%	“
Leccino	=	100 vs. 50%	Gucci et al., 2009
“	+	50 or 100 vs. 25%	“
Picual	=	Rainfed, 100%	Melgar et al., 2009

Table 2. Relative salt resistance of olive cultivars from different countries.

Cultivar	Salt resistance	Country	Author
Megaritiki	High	Greece	Therios and Misopolinos, 1988
Lianolia Kerkiras	“	“	“
Kalamon	“	“	Chartzoulakis et al., 2002
Frantoio	“	Italy	Gucci and Tattini, 1997
Arbequina	“	Spain	Benlloch et al., 1991
Picual	“	“	“
Lechin de Sevilla	“	“	Marin et al., 1995
Canivaro	“	“	“
Chemlali	“	Tunisia	Bouaziz, 1990
Amphissis	Medium	Greece	Therios and Misopolinos, 1988
Mastoidis	“	“	“
Koroneiki	“	“	“
Valanolia	“	“	Chartzoulakis et al., 2002
Adamitini	“	“	“
Maurino	“	Italy	Gucci and Tattini, 1997
Coratina	“	“	“
Moraiolo	“	“	“
Nabali Muhasan	“	Jordan	Al-Absi et al., 2003
Chalkidikis	Low	Greece	Therios and Misopolinos, 1988
Agouromaiki	“	“	“
Leccino	“	Italy	Gucci and Tattini, 1997
Cobrancosa	“	Spain	Benlloch et al., 1991; Marin et al., 1995
Pajarero	“	“	“

Figures

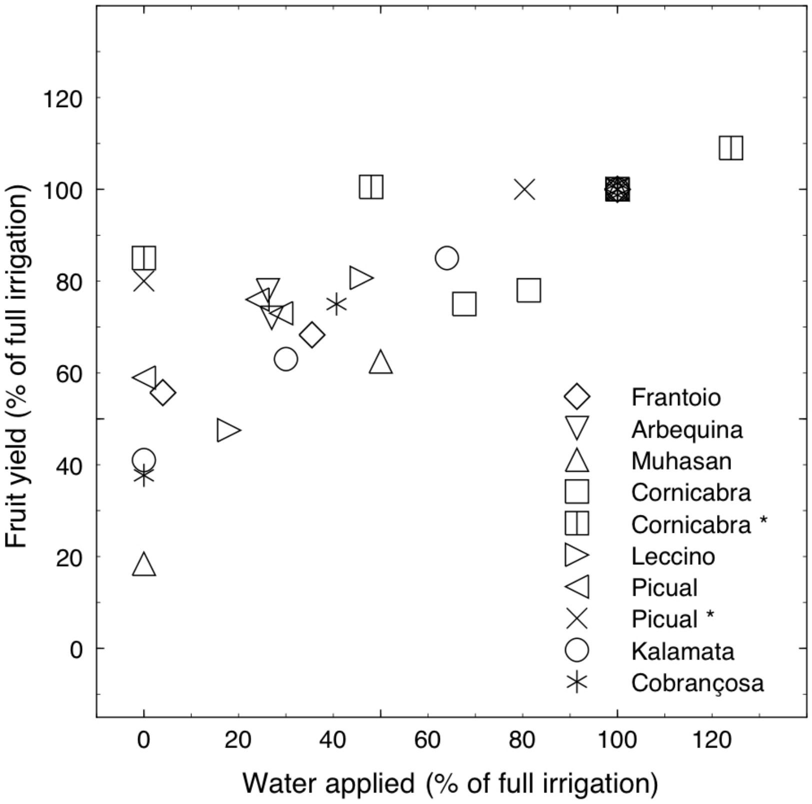

Fig. 1. The relationship between fruit yield and water applied by irrigation, both expressed as percentage of full irrigation, of olive trees of different cultivars derived from studies published in the last 10 years. Symbols are means of a minimum of two years (*n*), as reported in the legend below. Legend: ‘Frantoio’ (*n=2*) Caruso (2010); ‘Arbequina’ (*n=3*) Iniesta et al. (2009); ‘Muhasan’ (*n=4*) Lavee et al. (2007); ‘Cornicabra’ (*n=3*) Pérez-López et al. (2007); ‘Cornicabra’* (*n=2*) Gòmez-Rico et al. (2007); ‘Leccino’ (*n=2*) Gucci et al. (2007); ‘Picual’ (*n=3*) Moriana et al. (2003); ‘Picual’* (*n=9*) Melgar et al., (2008); ‘Kalamata’ (*n=2*) Patumi et al. (2002); ‘Cobrançosa’ (*n=2*) Fernandes-Silva et al. (2010).

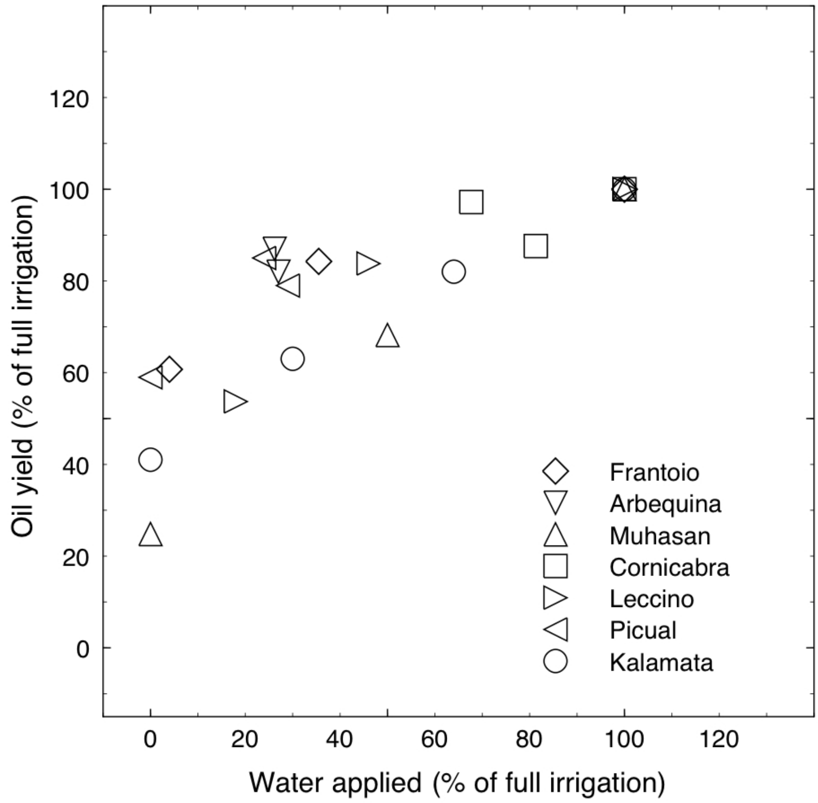

Fig. 2. The relationship between oil yield and water applied by irrigation, both expressed as percentage of full irrigation, of olive trees of different cultivars derived from studies published in the last 10 years. Symbols are means of a minimum of two years (*n*) as reported in the caption of Figure 1.