Highlights

- This is a review both on the response of olive to abiotic stresses and on new methods to improve crop performance
- The impact of stresses on the biennial olive cycle is first considered
- Then we summarized main morphological traits and physiological mechanisms relates to stress resistance
- Eventually we describe how the obtained knowledge is used to increase the crop performance

Understanding olive adaptation to abiotic stresses as a tool to increase crop performance

José-Enrique Fernández

Irrigation and Crop Ecophysiology Group
Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS, CSIC)
Avenida de Reina Mercedes n.º 10, 41012 Seville, Spain

Author details:
Phone: +34 954 62 47 11 (ext. 175) fax: +34 954 62 40 02
E-mail address: jefer@irnase.csic.es

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Most used symbols and abbreviations

A	net CO_2 assimilation rate
ABA	abscisic acid
C_a	ambient CO_2 concentration
C_c	CO_2 concentration in the chloroplast
C_i	CO_2 concentration in the intercellular air spaces within the leaf
C_s	CO_2 concentration next to the stomata
D_a	vapour pressure deficit of the air
$D_{\mathrm{l-a}}$	leaf-to-air vapour pressure deficit
DI	deficit irrigation, deficit irrigated
d.w.	dry weight
E_p	plant transpiration
E_s	soil evaporation
EC	electrical conductivity
$\mathrm{ET_c}$	crop evapotranspiration
$\mathrm{ET_o}$	potential evapotranspiration
FI	full irrigation, fully irrigated
f.w.	fresh weight
g_b	boundary layer conductance
g_c	cuticular conductance
G_c	canopy conductance
g_m	mesophyll conductance
g_s	stomatal conductance
$g_{\mathrm{s-max}}$	maximum stomatal conductance
GMT	Greenwich mean time
GSI	growing season index
HR	hydraulic redistribution
HS	period of high sensitivity to water stress
I_P	photosynthetic photon flux density
IA	irrigation amount
IN	irrigation needs
J_{max}	maximum rate of electron transport at saturating irradiance
K_c	crop coefficient

k_l	leaf-specific conductivity
L_v	root length density
LA	leaf area
LFDI	low-frequency deficit irrigation
N_a	nitrogen content per unit leaf area
P	atmospheric pressure
P_e	air entry pressure
P_eff	effective precipitation
P_{50}	xylem pressure at which 50% loss of hydraulic conductivity occurs
PAR	photosynthetically active radiation
PLC	percentage loss of conductivity
P-M	Penman-Monteith
p-v	pressure-volume
R_p	plant hydraulic resistance
r_s	soil surface resistance
RDI	regulated deficit irrigation
RuBP	ribulose-1,5-bisphosphate
RUE	radiation use efficiency
RWC	relative water content
$\mathrm{RWC}_\mathrm{tlp}$	relative water content at turgor loss point
S_D	stomatal density
SAR	sodium adsorption ratio
SDI	sustained deficit irrigation
SHD	super-high-density
SLW	specific leaf weight
T_a	air temperature
t_cw	cell wall thickness
T_l	leaf temperature
T_s	soil temperature
TPU	triose phosphate utilization
UV-B	ultraviolet-B
$V_\mathrm{c\text{-}max}$	maximum carboxylation efficiency
VC	vulnerability curve
WAB	weeks after bloom

WP	water productivity
WUE	water use efficiency
WUE_i	intrinsic water use efficiency
$\Delta\Psi$	gradient between soil and leaf water potential
ε	elastic modulus, modulus of elasticity
Ψ_l	leaf water potential
Ψ_p	leaf turgor potential
Ψ_pd	predawn leaf water potential
Ψ_s	soil water potential
Ψ_stem	midday stem water potential
Ψ_tlp	leaf water potential at turgor loss, or bulk turgor loss point
Ψ_x	xylem water potential
Ψ_π	leaf osmotic potential

ABSTRACT

In this work we give an overview of both morphological characteristics and physiological mechanisms responsible for the high adaptability of olive to harsh environments, and how this knowledge is currently used to design new sustainable and efficient crop management practices. We first describe the biennial vegetative and reproductive cycle of olive, and how these are affected by environmental conditions. Then we address main morphological, functional and physiological traits of olive that may contribute to stress tolerance. We also summarize innovative crop management practices that have been developed from our understanding of the mechanisms of response to abiotic stresses.

Keywords: crop management, hydraulic functionality, irrigation, photosynthesis, stomata, transpiration, water uptake, water productivity

1. Introduction

Olive has become a major crop in wide arid and semi-arid areas due to both its capacity to grow and produce acceptable yields under harsh environmental conditions and the demand for olive products, especially olive oil, which is considered by an increasing number of consumers as a key ingredient for a healthy diet. In addition, olive has shown a marked response to improved crop management practices. Both circumstances explain the substantial increase, since the 1980's, in the number of research groups focussed on understanding the biology of this species and its response to the environment, as well as in using the acquired knowledge to improve crop management practices and to design new cropping systems for more sustainable olive orchards. As a consequence, a substantial amount of information on olive biology and olive growing has been published in the last decades. Main findings have been summarized in comprehensive reviews on biology and physiology (Lavee, 1996; Connor and Fereres, 2005), response to environmental stimuli (Bongi and Palliotti, 1994; Sanzani et al., 2012), water use and irrigation (Fernández and Moreno, 1999; Gucci et al., 2012a; Carr, 2013). Other reviews focus on particular aspects, such as biology (Lavee, 1985, 1986; Fabbri and Benelli, 2000), drought stress (Xiloyannis et al., 1996), salinity stress (Gucci and Tattini, 1997; Ben-Gal, 2011), atmospheric pollutants and ultraviolet-B (UV-B) radiation (Sebastiani et al., 2002). The aim of this analysis is to highlight both the characteristics and the mechanisms responsible for the high adaptation of olive to harsh Mediterranean environments, and how this knowledge is currently used to improve sustainable crop management practices.

2. The olive biennial cycle

Commercial olive belongs to *Olea europaea* L., subspecies *sative*. The growth and reproductive cycle is biennial because flower induction occurs at summer, at the time of endocarp sclerification (Fernández-Escobar et al. 1992), but flower initiation and differentiation occurs during the next spring (Rallo and Cuevas, 2010). Following a period of winter dormancy, flower initiation occurs soon after bud burst, about two months before flowering (Fig. 1). Some buds are initiated and some of those differentiate to produce inflorescences. The crop load of the current year affects flower induction, by compounds released from developing fruits that are translocated back to the buds. The inhibition of floral induction by fruit and seed growth contributes to alternate bearing, a typical feature of olive. Years of intense fruiting ('on' years) tend to be followed by years of restricted flowering and reduced crop load ('off' years), causing the pattern of biennial flowering and yield. During the 'on' year, the developing fruits limit vegetative growth of the current year and flowering of the following year (Cuevas et al., 1994; Lavee, 1996). Results reported by Dag et al. (2010) suggest that flowering-site limitation, due to insufficient or immature vegetative growth during the 'on' years is the primary factor inducing alternate bearing in olive. Details on the phenological stages of olive are given in Sanz-Cortés et al. (2002).

2.1. Shoot growth

In winter, during dormancy, air temperature (T_a) values of -7 -8 ºC can cause damage to olive, although resistance to temperatures as low as -18 ºC have been reported (Sanzani et al., 2012). The threshold temperature below which frost damage occurs mostly depends on cultivar, plant age, sanitary and nutritional status. In the spring, during active shoot growth, olive is very sensitive to frost injury, and can suffer damage even at temperatures just below freezing, especially in tissues with high water content, such as the apexes of young leaves. It has been reported that organ sensitivity to low temperatures is in the order drupes > roots > new leaves > older leaves > twigs > buds (Fiorino and Mancuso, 2000; Graniti et al., 2011).

After a period of winter dormancy, and when T_a is above 12 ºC, shoot growth starts. In the northern hemisphere this occurs in early spring. Shoot growth rate and leaf size are cultivar-dependent and vary considerably according to plant age and vigour, and environmental conditions. A seasonal sequential change is apparent in current-year shoot (Lavee, 1996). In mid-summer, when $T_a > 30$ ºC, vegetative growth decreases and new leaves are progressively smaller. In autumn, following the reduction in T_a, a second period of rapid growth may occur, when soil water is newly available. Shoot growth is affected by crop load, since shoots and fruits compete for assimilates. In 'off' years, shoot growth rate is usually more constant than in 'on' years (Rallo and Cuevas, 2010). Shoot growth rate also depends on whether the bud from which the shoot originates is lateral or apical), and on the parent shoot age (Castillo-Llanque and Rapoport, 2011).

FIGURE 1 about here

2.2. Flowering

Olive blooms in spring, the exact date being related to the average daily T_a experienced approximately two months before (Rallo and Cuevas, 2010). Flowers are born on paniculate inflorescences of up to ~40 flowers each, which develop from buds in the leaf axis of the previous-season shoot (Lavee, 1996; De la Rosa et al., 2000). Consequently, flower number is determined by both auxiliary buds which differentiate into inflorescences and flower number per inflorescence. Subsequent changes from axillary bud to blooming inflorescence requires 2 to 3 months of growth and development, including elongation and branching of inflorescence axis, and formation and development of individual flowers (Rapoport et al., 2012). Olive inflorescences bear a mixture of hermaphrodite (perfect) and functionally staminate (imperfect) flowers due to pistil abortion (Reale et al., 2009). Imperfect flowers do not produce fruit. The proportion of imperfect flowers is cultivar-dependent (Rallo and Fernández-Escobar, 1985; Rosati et al., 2011) and it is affected by water availability and nutritional status (Uriu, 1960). Perfect flowers contain four ovules, two in each of two locules and are short-living. Pollen is produced in abundance over 5 days and individual stigmas remain receptive for 2 days. Flowering in individual trees lasts 10 days and in orchards for 20 days. The transformation of an olive ovary into a fruit requires, apart from fertilization, the development of a seed from at least one of the four ovules present in the ovary. Fruit set at 2 to 3 weeks after flowering may account for 10 to 15% of total flowers, but it decreases, to 7 to 10% in the following 4 to 5 weeks, i.e. 6 to 7 weeks after bloom (WAB). In years of heavy flowering, a fruit set of 1 to 2% can be adequate for a good commercial yield, 50% of flowers can be removed without affecting final fruit number (Lavee, 1996). Some ovaries develop parthenocarpically, i.e. without fertilization. The resulting fruits, named shotberries, are smaller and commercially unimportant because most abort quickly and few persist until harvest (Rapoport, 2010). Pollination is hindered by strong winds and rain, and may also suffer from high T_a or hot winds that desiccate pollen and stigmas (Connor and Fereres, 2005; Koubouris et al., 2009). Flowering is also affected by endogenous conditions. Ulger et al. (2004) reported that high levels of gibberellic acid GA_3 had an inhibitory effect on floral formation during the induction and initiation periods, and that high concentrations of gibberellic acid GA_4, abscisic acid (ABA) and cytokinins may have a positive effect on flower formation during the induction and initiation periods.

The effect of water deficit at different times from winter dormancy until flowering, and also at the time of flowering and initial fruit set, was studied in 3-year-old 'Picual' olive by Rapoport et al. (2012). Water deficit during winter dormancy had no effect on inflorescence and flower formation. During the period of inflorescence formation, water deficit caused significant reductions in flowering parameters. Water deficit during the floral development period caused lesser reductions in flowering parameters but hampered the pollination and fertilization processes. Water deficit during flowering and initial fruit set reduced pollination by hindering flower opening. Some compensation in fruit size occurred when the deficit treatments resulted in lower fruit number, but it was insufficient for maintaining full fruit production. Typical olive adaptive responses and detrimental effects of water deficit during the pre-flowering and flowering periods were described by Pierantozzi et al. (2013). Both flowering and fruit set are strongly affected by T_a (Sanzani et al., 2012), so that olive flowering date is a reliable indicator of climatic warming (Osborne et al., 2000; Bonofiglio et al., 2009). The effect of T_a on flowering, however, is not clear. Temperatures between 2-4 ºC and 15.5-19 ºC were reported by Denney and McEachern (1983) as providing an optimum balance between the chilling signal (vernalization) that releases induced buds for further development and the warm conditions that supports the associated growth, as higher temperatures reverse the chilling effect (devernalization). Chilling requirement is not absolute because olive flowers and produces fruits in various subtropical locations where vernalization conditions (as defined above), do not occur (Connor and Fereres, 2005; Searles et al., 2011). Yields are usually low in areas with T_a above olive requirements. Ayerza and Sibbet (2001) evaluated the suitability of new sites for olive production in Argentina, where the maximum number of vernalizing days is 110, while in Spain or Italy 150 vernalizing days per year are common. They concluded that in Argentina and in other olive expanding areas, greater damage was produced due to high T_a at flowering more than by low T_a. A common practice in that region is indeed to suspend irrigation during the winter months, because water stress promotes flowering once irrigation resumes in spring.

2.3. Fruit development

Olive is a drupe consisting of fleshy pericarp (pulp) and woody endocarp (stone) that encloses a single seed. The pericarp has an outer epicarp composed of a layer of small cells rich in chloroplasts, and an inner mesocarp composed of parenchymatous cells rich in oil, the size of which increases radially from outside to inside (Sánchez, 1994). Olive oil is present in both mesocarp and seed. Part of the oil present in the mesocarp is imported from other plant organs, whereas the rest is formed *in situ*, due to fruit CO_2 assimilation. Oil in the seed is imported, and used for nourishing the embryo during the initial stages of germination. The oil in the mesocarp is for attracting animals, which then contributes to seed dissemination (Sánchez 1994). Mesocarp volume is important for oil production, since this tissue is where up to 98% of the oil accumulates. The oil content of olives can reach over 30% fresh weight (f.w.) at the end of ripening period.

Most of the endocarp and mesocarp cells are produced between 4 and 10 WAB period (Rallo and Rapoport, 2001; Rapoport, 2010). From that time until fruit maturity, considerable cell expansion occurs, and an additional 10% to 40% of mesocarp cells may still be produced, depending on cultivar. During the first half of the developmental period the fruits increase their weight at more or less linear rates, so that at ~ 25 WAB they reach final size (Fig. 1). Ninety per cent of the endocarp growth occurs by 8 WAB (Rapoport et al., 2004), and then cells become highly lignified in contrast to the basically parenchymatic oil-storing cells of the mesocarp. Water deficit at the period of 4 to 10 WAB might highly affect both cell number and cell size (Rapoport et al., 2004; Gucci et al., 2009). Hammami et al. (2011) reported that excessive water stress in the first 8 WAB may lead to reduce cell number in olive fruits. Thus the final fruit f.w. and volume can be reduced if water supplies are not enough at that period of high sensitivity of the olive fruit to water stress (Fig. 1). The effect of water availability on endocarp development was further investigated by

Hammami et al. (2013). Maximum mesocarp-to-endocarp ratio is an important feature for olive fruit quality for both table consumption and oil production. Irrigation increases the mesocarp-to-endocarp ratio when compared with rain-fed trees (d'Andria et al., 2004; Gómez-Rico et al., 2007; Lavee et al., 2007), but this ratio is not affected much at mild water stress (Gucci et al., 2009; Lavee et al., 2007).

Oil accumulation begins from ca. 8 WAB. Oil accumulation in the seed is relatively fast and is completed in about 10 weeks. In the pulp the oil content increases more slowly and takes some 20 weeks or more to reach a plateau (Lavee and Wodner, 1991). The oil accumulation pattern changes considerably under stressing conditions. The mesocarp is more responsive to water deficit than the endocarp. Gucci et al. (2009) reported that both the fruit f.w. and dry weight (d.w.) responded to water status, but f.w. was more sensitive, for both endocarp and mesocarp. Both fruit size and oil content in the mesocarp were affected by crop load. High crop loads decreased fruit f.w. at harvest in fully irrigated (FI) and deficit irrigated (DI) trees, but not in severely stressed olive trees (Gucci et al., 2007). This may explain why irrigation affects fruit size differently in 'on' and 'off' years (Moriana et al., 2003; Lavee and Wonder, 2004). The ripening process, characterized by a change in the colour of the fruit, starts ca. 30 WAB, when the rate of oil accumulation is reaching a plateau (Fig 1).

The importance of sunlight irradiance for olive production is long known. Ortega-Nieto (1962) reported greater oil content in illuminated than in shaded fruits. Recently, Gómez-del-Campo and García (2012) reported that fruits from the illuminated canopy areas produced stable oil, rich in phenols saturated fatty acids. Knowledge on the accumulation of photosynthates and their redistribution within the plant are crucial for developing good pruning practices in olive orchards (Gucci and Cantini, 2000), as well as for designing new olive growing systems such as hedgerow olive orchards with high plant densities, also called super-high-density (SHD) orchards (Rius and Lacarte, 2010).

Early frosts in autumn, before harvesting, can dehydrate the drupes and cause skin shrivelling (-0.4 ºC), permanent fruit damage, fruit drop (-1.7 ºC), and fruit freezing (-3 ºC) (Sanzani et al., 2012). Damaged fruit parts are frequently colonized by pathogens, which penalizes oil quality. However, slight frost damage can increase oil extractability, because fruit water content decreases. Water stress during fruit development affects ripening date, thus favouring early harvesting and minimizing risk of frost damage. Contrasting results of the effect of water stress on ripening date, however, have been reported. Motilva et al. (2000), Berenguer et al. (2006) and Gucci et al. (2007) showed that ripening was delayed by irrigation, whereas irrigation caused earlier ripening in other circumstances (Morales-Sillero et al., 2013; García et al., 2013).

3. Morphological adaptations to abiotic stresses

The high capacity of olive to grow under harsh conditions is due to morphological characteristics as well as to physiological mechanisms, related with escape, avoidance and tolerance components of stress resistance. In this section, we address the morphological adaptations olive has developed to survive and yield under 'limiting' conditions. Main physiological mechanisms related to stress resistance are detailed in the next section.

3.1. The root system

The olive root system is adapted to scarce and intermittent rainfall events typical of Mediterranean areas. A large root portion, in fact, grows, more or less, parallel to soil surface, thus exploring top soil layers (Fernández et al., 1991; Searles et al., 2009). In aerated soils of light texture, however, olive roots may reach depths of 6-7 m (Lavee, 1996). Olive roots are sensitive to hypoxia, although olive root system can adapt to heavy, unaerated soils by developing a shallow and wide root system (Lavee, 1996). In dual soils, characterized by sandy top layer and clayey bottom layer of high resistance to penetration, roots may only explore top layer, and penetrate deeper layers due to soil cracks and favourable aeration when soil dries (Diaz-Espejo et al., 2012). For olive trees with localized irrigation, the greatest root length densities (L_v) of fine (Ø < 0.5 mm), active roots, are found in wetted soil volumes close to the drippers, with a favourable balance between air and water for root growing (Fernández et al., 1991; Searles et al., 2009). For rain-fed trees, the greatest L_v and root activity values are usually found at less than 0.5-0.6 m from the trunk and between 0.15-1.0 m in depth (Abd-El-Rahman et al., 1966; Fernández et al., 1991). The high concentration of active roots in superficial soil volumes close to the trunk increases the efficiency of the olive tree in absorbing rainfall water that runs down the stem (Gómez et al., 2001).

The capacity of olive to take up water and nutrients not only depends on root distribution, but also on root growth dynamics and activity. Sap flow methods are currently used to quantify both absolute values and the dynamics of water uptake by single roots (Moreno et al., 1996; Fernández et al., 2001; Nadezhdina et al., 2007) (Section 4.1.2).

Fernández et al. (1992) evaluated the effect of irrigation on olive root growth and activity. They showed that irrigation may shorten the period for orchard establishment, and deeply influences relations between the above-grown and the below-ground tissues. The growth dynamics of olive roots also depends on sink-source competition, which establishes between aerial and subterranean organs throughout the year (Celano et al., 1998). Water supply, tree age, plant density and soil characteristics greatly affect the root/canopy ratio. Rain-fed olive trees usually show greater root/canopy ratios than irrigated trees, since they have to explore larger soil volumes to collect similar water and nutrient amounts (Celano et al., 1999; Fernández et al., 1991, 1992). The capacity of the olive tree to explore big soil volumes can be markedly curtailed both by the soil and tree characteristics conditions and the orchard design and management (Fernández et al. 2008a; Diaz-Espejo et al., 2012).

An example of root 'plasticity' in olive to adapt to soil conditions is given in Rewald et al. (2011a). They evaluated salt tolerance of 'Barnea', 'Arbequina' and 'Proline', and reported that fine roots of 'Barnea' trees irrigated with saline water (electrical conductivity, EC = 7.5 dS m^{-1}) increased specific conductivity due to the development of high conduit diameter and root biomass. Additional results on sap flow and carbon allocation (Rewald et al. 2011b) show that under moderate salinity, the tolerant 'Barnea' was to sustain higher fine root biomass and root sap flow density than 'Proline' trees. Soil temperature (T_s) also influences root functioning. In most olive growing areas, low T_s at winter may induce tree water deficit even at optimal water supply. In an experiment with FI 'Picual' potted saplings exposed to T_s < 10 ºC, both the leaf water potential (Ψ_l) and the stem water potential (Ψ_{stem}) decreased, and root hydraulic resistance increased. At T_s < 6.4 ºC, stomatal conductance (g_s) also decreased. The authors speculated with these effects being due to temperature-driven changes in ABA, membrane permeability, enzymatic activity and water viscosity (Pavel and Fereres, 1998).

3.2. The stem

The bark and wood of olive stem may differ greatly depending on environmental conditions. Under dry conditions stem develops a thick cork layer covering the living bark tissues, thus protecting against sunburning. In mature, rain-fed 'Manzanilla' trees bark thickness 6-8 mm was detected, of which the outer 3-4 mm consisted of death tissues. Below the bark there is the phloem, the cambium, and the xylem. The sapwood, i.e. the outer part of the xylem through which water flows from roots to leaves, shows high azimuthal variability, ranging from 12 mm to 53 mm in the same tree (Fernández et al., 2006a, Giorio and Giorio, 2003; Nadezhdina et al., 2007). Radial sap flow profiles within the same tree have also been reported to change greatly depending on water stress. When the stress increases, greater flows are recorded deeper into the xylem (Fernández et al., 2001). The authors hypothesized that both stomatal control in young leaves and embolism within the outer xylem vessels were responsible for the loss of flow in the xylem vessels of the outer annuli. Nadezhdina et al. (2007) also reported great radial changes on sap flow rate in olive trunks, and hypothesized that they reflects a vertical distribution of water uptake that varies with water availability at different soil layers.

3.3. The leaf

The olive leaf is hypostomatous, i.e. stomata occur on abaxial leaf surface. This is typical of plants growing in dry and hot areas (Hetherington and Woodward, 2003). Leaf is also homobaric, i.e. displays a uniform stomatal distribution (Marchi et al., 2008). In the adaxial surface the epidermis is covered by a waxy cuticle. Palisade parenchyma usually consists of two- three highly-packed layers of elongated cells, which are interspaced by tricosclereids (Fig. 2). Spongy mesophyll anatomy greatly depends on leaf water status (Ehrenberger et al., 2012). Leaves suffering from water deficit display palisade-like cells just below the abaxial epidermis (bifacial-like leaves) (Chartzoulakis et al., 1999; Bacelar et al., 2004).

In the lower, abaxial surface of the leaf there are the stomata hidden by numerous trichomes, thus limiting water loss. Well-developed trichome layer may also increase water-use efficiency through the increase in leaf boundary-layer resistance (Pallioti et al., 1994). Hairy abaxial surface limits sunlight absorption: absorption of incident photosynthetically active radiation (PAR) in 'Manzanilla' leaves is 97% or 63% for adaxial and abaxial surface, respectively (Diaz-Espejo, 2000). Olive leaves display paraheliotropism, i.e. leaf movements aimed reduce light interception and then photoinhibition (Schwabe and Lionakis, 1996; Natali et al., 1999; Werner et al., 2002). The small size of olive leaves also contributes to high adaptation to atmospheric demand, e.g., vapour pressure deficit of the air (D_a) being the main driving variable for plant transpiration (E_p) (Tognetti et al., 2009; Diaz-Espejo et al., 2012) This explains the effective stomatal control on E_p usually detected in olive (Section 4.3). Leaf dehydration is also limited by a negligible cuticular conductance (g_c). Our measurements of g_c in leaves of

'Arbequina' showed that g_c ranged from 1 to 3 μmol m^{-2} s^{-1}, whereas g_s was 300 μmol m^{-2} s^{-1}. This confirmed negligible g_c values due to waterproof capacity of olive leaf cuticle (Fernández and Moreno, 1999; Connor and Fereres, 2005).

In olive leaves may be up to 3-year-old. Aging modifies leaf characteristics and response to environmental stimuli. Leaf thickness, total chlorophyll concentration, and photosynthetic capacity increases during leaf development (Marchi et al., 2008). Olive leaves become fully expanded usually in 3-4 weeks. A great proportion of stomata are not fully developed prior the leaf reaches 50% of final size (Lavee, 1996; Marchi et al., 2008). Bongi et al. (1987) reported an increase in A over first two months of leaf life, a plateau from 2 to11-13 months, and decreases of ~50% when the leaf was 2-year-old. Marchi at al. (2005) observed that net daily A was negative in young expanding leaves, and leaves became source leaves when the size was approximately at 30% of the size at full development.

Environmental conditions during development also have marked influence on olive leaf features. Leaves developed under drought usually have more but smaller stomata than leaves under well-watered conditions (Larcher, 1995). They also have higher specific leaf weight (SLW), as a consequence of increased density and thickness (Centritto, 2002). The greater leaf tissue density may contribute to drought tolerance, because of greater resistance to physical damage driven by desiccation (Mediavilla et al., 2001). Similar results have been reported by Boughllleb and Hajlaoui (2011).

FIGURE 2 about here

4. Physiological adaptations to abiotic stresses

Main functional and physiological mechanisms of adaptation to environmental constrains of Mediterranean climate in olive have been summarised in Figure 3, which includes equations to estimate E_p. Equation 1 quantifies E_p at daily central hours, when the transpiration rate is relatively constant, i.e. from 09:00 to 15:00 Greenwich mean time (GMT) for olive growing in typical Mediterranean areas. In this equation, Ψ_s is the 'effective' soil water potential at the root surface and Ψ_l is the 'effective' leaf water potential for the whole canopy (Jones, 1983).The equation shows that a minimum $\Psi_s - \Psi_l$ gradient ($\Delta\Psi$) must be achieved for water to flow from roots to leaves, thus allowing plant transpiration. During soil drying $\Delta\Psi$ may reach a threshold value for inducing embolism (Tyree and Sperry 1989). We prefer refer as to threshold value for the loss of hydraulic conductance, since the increase in the plant hydraulic resistance (R_p) is not merely due to increased number of embolized xylem vessels. The effect of water stress on other features involved in plant hydraulic functionality, such as aquaporins, is also significant (Secchi et al., 2007). Estimating Ψ_s is difficult. When water is homogeneously distributed in the soil Ψ_s is assumed similar to pre-dawn water potential measured in basal leaves (Ψ_{pd}). This assumption, however, is not true when water is not heterogeneously distributed in the rhisozphere, e.g., in olive under localized irrigation: Ψ_{pd} values are usually biased towards the wettest part of the root zone (Jones, 1983). Ψ_l is determined by integrating leaf water potentials of sunlit and shaded leaves, following estimate of both types of leaves in the canopy (Moreshet et al., 1990; Diaz-Espejo et al., 2002).

Equation 2 shown in Fig. 3 links E_p with canopy conductance (G_c), leaf-to-air vapour pressure deficit ($D_{l\text{-}a}$) and atmospheric pressure (P). It can be used to estimate leaf transpiration, just replacing G_c with g_s. Both conductances strongly depends on stomatal control, an effective mechanism to withstand drought operating in olive as well as in other plants inhabiting arid and semi-arid areas. Under water stress, plants minimize the loss of hydraulic conductivity by closing stomata. This helps the xylem water potential (Ψ_x) to remain above the safety threshold for loss of hydraulic conductance. Equations 1 and 2 illustrate that g_s, Ψ_x and R_p are mutually influenced and relate with E_p. The link between these variables, together with their feedback loops and feed-forward regulations is still matter of debate (Buckley 2005). Nonetheless, here we summarize main mechanisms that relate with these variables and that confer to olive a high capability to keep Ψ_x above safe limits. Comprehensive analyses of the effect of above mentioned mechanisms operating in olive have been given in Tognetti et al. (2009) and Diaz-Espejo et al. (2012).

FIGURE 3 about here

4.1. Water uptake from drying soils

The pressure-volume (*p-v*) curve relates Ψ_l vs. water volume in drying leaves. From the analysis of *p-v* curves we can derive six key leaf parameters related with stress tolerance (Barlett et al., 2012). One relevant parameter is leaf water potential at turgor loss, or at bulk turgor loss point (Ψ_{tlp}, MPa), classically used to assess drought tolerance. Plants with low Ψ_{tlp} tend to maintain g_s, hydraulic conductance, photosynthetic gas exchange and growth as the soil dries. Ψ_{tlp} defines the permanent wilting point. For many species the permanent wilting point occurs at ~ $\Psi_s = -1.5$ MPa (Veihmeyer and Hendrickson, 1928). In olive, however, this value ranges from ~ -2.5 MPa (Xiloyannis et al., 1996; Dichio et al., 2003) to ~ -3.5 MPa (Lo Gullo and Salleo, 1988; Dichio et al., 2005). However, olive may transpire and photosynthesize at Ψ_{tlp} of -5.3 MPa (Perez-Martin et al., 2009) and even of -8.0 MPa (Moriana et al., 2003). This conforms to well-known capacity of olive to take up water from drying soils (Fernández and Moreno, 1999; Connor and Fereres, 2005, see below for details).

4.1.1. Osmotic adjustment and elastic module

The leaf water potential depends on the turgor (Ψ_P) and osmotic potentials (Ψ_π), being $\Psi_l = \Psi_P - \Psi_\pi$. Time course of Ψ_π under increasing water stress shows that olive is capable of large osmotic adjustment, leading to high values of $\Delta\Psi$ (Eq. 1, Fig. 3). Osmotic adjustment must not be confused with the passive (i.e. driven by tissue dehydration) increase in solute concentrations under increasing water stress or salinization. Active osmotic adjustment occurs via net accumulation of solutes to decrease Ψ_π (Section 4.5). In an experiment with 2-year-old 'Coratina' trees, Dichio et al. (2005) reported, for severely stressed trees ($\Psi_{\mathrm{pd}} = -5.35$ MPa), that osmotic adjustment ranged from 2.4 MPa at 05.00 h to 3.8 MPa at 18.00 h. Previously, Dichio et al. (2003) had reported that leaf osmotic potentials at full turgor and at turgor loss decreased from -2.06 ± 0.01 MPa and -3.07 ± 0.16 MPa in controls to -2.81 ± 0.03 MPa and -3.85 ± 0.12 MPa in the most stressed plants. Dell'Amico et al. (2012) evaluated the effect of increased water stress at mid-summer (between HS2 and HS3 periods described in Fig. 1) in 43-year-old 'Manzanilla'. They explored changes in water relations of fruit and leaves, including Ψ_π, and suggested that a valued of $\Psi_{\mathrm{stem}} \approx -1.8$ MPa could be considered as a reference for DI in olive.

At cellular level, turgor pressure is given as the difference between pressures inside and outside of cell wall. When cell wall is rigid, water potential and its components change rapidly following loss of water. The wall rigidity is described by the elastic modulus or modulus of elasticity (ε) of the cell. Wall rigidity measured in tissues is termed bulk modulus of elasticity of the cell (Jones 1983). In olive ε tends to increase with drought.

Bongi and Palliotti (1994) reported that elasticity in olive leaf tissues decreased with leaf ageing, in turn affecting ε. These authors reported that in olive leaves at 87.5% of maximal cell volume, ε was 8.4 MPa in young leaves and 22.5 MPa in mature leaves. Dichio et al (2003) reported ε to increase from 11.6 ± 0.95 MPa in fully irrigated to 18.6 ± 0.61 MPa in stressed plants. It is assumed ε contributes to maintain Ψ_P in water-stressed plants. The role of ε in drought tolerance has been recently examined in Barlett et al. (2012). Authors compared five hypotheses to clarify the relationship between high ε, Ψ_{tlp} and drought tolerance, to conclude that high ε allows cells to maintain high relative water content at loss point (RWC_{tlp}), at very negative osmotic potential at full turgor. This confers to plants tolerance to low Ψ_s and prevents cell dehydration and shrinkage. Therefore, during water stress, osmotic adjustment-induced reduction in Ψ_{tlp} must be paralleled with changes in to maintain high RWC_{tlp}. The work of Diaz-Espejo et al. (2012, 2013) illustrate the importance of considering Ψ_π and ε for establishing water stress related behaviours in olive, as well as for simulating transpiration.

4.1.2. Hydraulic redistribution

The movement of water through plant roots from moist to dry soil layers, or hydraulic redistribution (HR) (Burgess et al., 1998) is crucial for the survival of species in arid environments. Hydraulic lift is the nocturnal uptake of water by roots from deep, wetter soil layers and the release of this water from shallow roots into drier, upper layers of soil. Lateral flows and downwards flows in the root system may also occur, depending on the soil water distribution at the root zone. These types of reverse flow are termed HR (Fernández and Clothier, 2002). The process is believed to be passive, driven by soil and root water potential gradients (Prieto et al., 2012). External features in and around roots, however, influence HR. Thus, resistance to water flow through roots depends partly on aquaporins (McElrone et al., 2007) and architectural- morphological root traits, as well as root history. For example, HR occurs in species with dimorphic root systems, as occurs in fruit tree species including olive, whereas monomorphic species do not usually exhibit HR (Grigg et al., 2010). HR contributes in maintaining root hydraulic conductivity in drying soils and in repairing embolized xylem vessels (Domec et al., 2006). HR allows root survival and root growth in dry soil layers, which are usually superficial layers rich in nutrients, microorganisms and organic matter as compared with deeper, wetter layers (Domec et al., 2010).

HR was recently found to operate in olive Nadezhdina et al. (2012) and Ferreira et al. (2013). Nocturnal reverse flow in shallow roots of the rain-fed tree started at the beginning of June, as soon as the top soil layer explored by the root dried up, and increased, both in magnitude and duration, along the summer. High night flows were recorded in the deep root. The authors concluded that olive trees under dry-farming conditions use deep water sources for transpiration as well as to water superficial roots in the dry top soil layers. Ferreira et al. (2013) explored the role of lignotubers in the same rain-fed 'Cobrançosa' orchard and its connections with root dynamics. They reported marked changes on the relative contribution of deep and shallow roots, including hydraulic lift in shallow roots before the arrival of the rainy season.

FIGURE 4 about here

4.2. Vulnerability to embolism

During drought, leaf transpiration often exceeds the water transport capacity of the xylem. Then Ψ_x drops and the risk for cavitation within the xylem conduits increases. Cavitation or air-seeding in plants is caused by the aspiration of air into the transpiration stream through the pit membrane. The wall of olive xylem vessels has numerous pits from which water and air can flow between adjacent vessels (Fig. 5). Within each pit there is a porous membrane. When a vessel is embolized, air is prevented from moving into the neighbour vessel by the capillary force of the air-water meniscus in the pores of the pit membrane. Air will be aspirated into the adjacent, functional vessel when the pressure difference across the meniscus exceeds the force caused by the sap tension in the vessel (Sperry and Tyree, 1988). If the tension in the sap increases further, the air bubble expands and the conduit is simultaneously drained of water. Ultimately, a mixture of air and vapour fills the entire conduit to create embolism, which blocks water transport in the conduit. Because embolism reduces the number of functional conduits, R_p increases. Under drought conditions, therefore, higher tensions predispose the xylem to further cavitation events that can potentially lead to embolism and plant death (Tyree and Sperry, 1988; Pittermann, 2010). However, not all cavitation events cause embolism, which explains the use of cavitation resistance and vulnerability to cavitation being currently replaced with embolism resistance and vulnerability to embolism.

Vulnerability curves (VCs) are typically used to evaluate the vulnerability to embolism. These curves express the percentage loss of conductivity (PLC) due to embolism in response to increasingly negative Ψ_x. Vulnerability curves can be generated from samples taken from any conductive organ of the plant, such as roots, stems and leaves. The VCs show the xylem pressure at which samples exhibits 50% loss of hydraulic conductivity. This is referred to as the P_{50} or cavitation pressure. The P_{50} value is used to compare embolism resistance between plant organs or species. Another parameter of interest that can be derived from VCs is the air entry pressure (P_e), which indicates the threshold xylem pressure at which loss of conductivity begins to increase rapidly (Meinzer et al., 2009). Torres-Ruiz et al. (2013a) worked with 41-year-old 'Manzanilla' olive trees under contrasting water treatments. Figure 6 shows the calculated VCs for rain-fed trees and for trees under localized irrigation, with daily supplies to replace 100% of the crop evapotranspiration (ET_c). The VCs yielded a P_e value of ca. -1.3 MPa. Water treatments did not influence the vulnerability to embolism, which agree with anatomical observations showing no significant effects of water status on either vessel-diameter distribution or vessel density. Other authors, however, have shown that olive under different water regimes display differences in xylem structure and function (Bacelar et al., 2007a; Lopez-Bernal et al., 2010; Rossi et al., 2013).

Woody plants growing in Mediterranean-type ecosystems usually show a high resistance to drought-induced embolism (Maherali et al., 2004). Olive displays low hydraulic conductivity and is able to withstand water potentials below Ψ_{tlp} with minor seasonal xylem embolism (Salleo and Lo Gullo, 1983; Torres-Ruiz et al., 2013a). A trade-off may exist between xylem vulnerability to embolism and xylem hydraulic conductance (or wood construction cost, Martinez-Vilalta et al., 2002; Hacke et al., 2006). It has been reported that the diameter of the xylem vessel, together with Ψ_x, highly determines the occurrence of embolism and, consequently, the value of R_p. The vulnerability to embolism is determined, however, by the diameter of the intervessel pit membrane pore, rather than by that of the xylem vessel (Tyree and Sperry, 1989). In fact, the pit area hypothesis (Wheeler et al., 2005) states that the Ψ_x value corresponding to P_{50} is determined by the largest pit pore in the total pit area of a vessel. Recent evidence shows that water in the xylem vessels under tension contain a large number of nanobubbles which size depends on the structure and porosity of the pit membrane, and that these nanobubbles can explode, leading to embolism, or can shrink, causing nocturnal embolism repair (Weijs et al., 2012; Brodersen et al., 2013). It seems that the origin and size of the nanobubbles depend on the structure of the pit membrane, rather than on absolute pore diameters (Jansen et al., 2009).

Equation 1 (Fig. 3) can be used to calculate R_p. Larsen et al. (1989) followed this approach and calculated R_p values, in MPa μg^{-1} cm^2 s, of 0.182 for apple, 0.319 for peach, 0.329 for grape, 0.465 for olive, and 0.511 for apricot. They stated that high value of R_p in olive, together with stomatal closing, may account for the low transpiration losses per unit leaf area (LA) measured in this species. Bongi and Pallioti (1994) mentioned that large water potential differences between leaves and roots usually found in olive might reflect a strong resistance to water movement. In field experiments with well-irrigated trees, in which $\Psi_s \approx \Psi_{pd}$, we have observed that the drop in water potential from leaves to roots is usually greater than 2 MPa, with a maximum difference of about 4 MPa (unpublished data).

FIGURE 5 about here

FIGURE 6 about here

4.3. Stomatal control of gas exchange

The role of stomata is to regulate the entry of sufficient CO_2 for optimal photosynthesis while conserving water inside the plant. As in many other plants well adapted to dry areas, stomatal closure in olive limits transpiration and avoids risky Ψ_x for hydraulic functioning (Fernández et al., 1997; Tognetti et al., 2009; Boughalleb and Hajlaoui, 2011). As already mentioned, the relationships among Ψ_l, g_s, E_p and R_p, and of these variables with environment, are still in the dark. There are feedback and feed-forward mechanisms involved (Chaves et al., 2003; Lovisolo et al., 2010), and differences between cultivars have been reported (Fernández et al., 2008b). It appears that stomatal guard cells respond by negative feedback to Ψ_p, which is related with Ψ_l and then with Ψ_x. Thus, the plant can operate near the embolism threshold, generating the required $\Delta\Psi$ for transpiration and at the same time avoiding the risk of excessive R_p (Eq. 1, Fig. 3). However, is unclear whether this equilibrium is achieved by passive feedback, active feedback, feed forward, or some combination of these processes (Buckley 2005). A metabolically mediated feedback response of stomatal guard cells to water status in their immediate vicinity ('hydro-active local feedback') is likely the best explanation for many well-known features of hydraulically related stomatal behaviour. Both apparent feedforward response of stomata to D_a and isohydric behaviour observed in many cases, may be explained through the juxtaposition of hydro-active local feedback and hysteretic and threshold-like effect of Ψ_x on R_p. The matter is further complicated by long-distance and short-distance signalling mechanisms acting on stomata (Sections 4.3.2 and 4.3.3). In other words, trees respond to drought by processing information from simultaneous, often conflicting, and sometimes rapidly changing signals, related with several mechanisms acting in a nested hierarchy and occurring at different time scales (Hetherington and Woodward, 2003; Limousin et al., 2010). Below we give an overview of the most relevant stomatal responses to both exogenous and endogenous plant conditions.

4.3.1. Response of the stomata to soil water and atmospheric demand

The available soil water has great influence on stomatal closure. In FI 'Manzanilla' trees under localized irrigation, Cuevas et al. (2010) recorded a maximum stomatal conductance ($g_{s\text{-max}}$) of 0.29 mol m^{-2} s^{-1}, a value similar to that reported by Diaz-Espejo et al. (2006) for the same cultivar growing under non-limiting conditions. In trees under dry-farming conditions, $g_{s\text{-max}}$ was only 0.13 mol m^{-2} s^{-1}. Values of Ψ_l measured at midday (-1.31 MPa for irrigated trees, -1.51 MPa for rain-fed trees) showed no significant differences in leaf water status in differentially irrigated trees. This implies that effective control of Ψ_l by stomatal closure operates in rain-fed trees. Torres et al. (2013a) observed stomatal control of transpiration in irrigated trees, such that Ψ_l did not change along the day, despite of two-fold increase in D_a from morning to afternoon. In irrigated trees Ψ_l was maintained around 1.4-1.6 MPa, i.e. above critical values for losing xylem functionality (Fig. 6). These results illustrate the role of stomatal closure in avoiding marked decrease in $\Psi_{l,}$ and consequently in Ψ_x, under conditions of low soil water and high evaporative demand. Stomatal closure is a key mechanism that operates in olive to minimize loss of xylem functionality during the dry season. However, the capacity of stomata to regulate transpiration is lost when soil water is severely depleted: severe water stress overrides olive functions, including the control of gas exchange driven by stomata (Moriana et al., 2002). In their rain-fed trees, in fact, Torres et al. (2013a) found no effective regulation of Ψ_l by stomatal closure when Ψ_l was as low as -4.8 MPa.

Available soil water as well as its distribution at the root zone affect stomatal closure. Cuevas et al. (2010) and Torres et al. (2013a) observed stomatal regulation of transpiration in plants under localized irrigation (LI treatment) which, despite of receiving daily water supplies to replace 100% of ET$_c$, had a fraction of their roots under soil-drying conditions. Morales-Sillero et al. (2013) worked in the same orchard and considered an additional treatment in which the whole root zone was kept under non-limiting soil water conditions all throughout the irrigation season (Pond treatment). They reported similar values of Ψ_l in both LI and Pond trees, but the LI trees usually showed lower values of g_s. The authors agreed with Cuevas et al. (2010), who reported that olive showed a near-isohydric behaviour, similar to that reported for other woody crops is the area such as grapevine (Schultz 2003).

Main driving meteorological variable for stomatal opening in olive is photon flux density (I_P) and D_a (Fernández and Moreno, 1999). Upper-bound relationships between g_s and I_P and D_a have been analysed in Fernández et al. (1997) for 'Manzanilla'. Authors found that relatively low levels of I_P, ~500 µmol m^{-2} s^{-1}, were enough to achieve maximum potential values of g_s. Decreasing g_s values were observed from D_a over the range 1 kPa to 3.5 kPa. At greater D_a stomata remained partially open. High values of g_s were observed in the morning, during the opening phase, than in the afternoon at similar D_a and I_P. This may result from maximum I_P occurring early in the day as compared with daily maxima in D_a. The fact that D_a is the main driving variable for stomatal closure in olive is true except in winter. In winter, soil temperature (Gimenez et al., 1996), and factors related to root functioning (Fereres et al., 1998), may depress Ψ_l and g_s values, despite high Ψ_s and relatively low atmospheric demand. Moriana et al. (2002) derived relationships between D_a and g_s at midday, for 'Picual' under different drought levels. Stomatal conductance decreased linearly as D_a increased, for trees suffering from low ($\Psi_l > -1.65$ MPa) to high (-2.5 MPa $> \Psi_l > -4.0$ MPa) water stress. For trees with $\Psi_l < -4.0$ MPa D_a did not effect stomatal closure, and similar g_s (< 25 mmol m^{-2} s^{-1}) were found for D_a in the range 2-7 kPa. Diaz-Espejo et al. (2006) reported t maximum g_s in 'Manzanilla' growing in southwest Spain when soil was around field capacity and values of I_p, leaf temperature (T_l) and D_a of 1600 µmol m^{-2} s^{-1}, 25 ºC, and 1 kPa, respectively.

4.3.2. Stomatal conductance, plant water status and transpiration

In experiments with olive saplings in pots, i.e. under highly uniform soil water distribution, robust Ψ_l vs. g_s relationships have been observed: g_s decreases progressively as Ψ_l becomes more negative (Guerfel et al., 2009; Boughalleb and Hajlaoui, 2011). In trees under field conditions, however, correlations between Ψ_l and g_s are much weaker. This can be due to stomatal response to variable distribution of soil water, reported above.

Additionally, water potential of stomatal apparatus differs from the bulk Ψ_l (Fernández and Moreno, 1999). Correlations between Ψ_{stem} and g_s are more robust as compared with Ψ_l vs g_s, in several fruit tree species (Naor et al., 2004, 2006). For olive, significant, non-linear correlations between Ψ_{stem} and g_s have been reported, in both potted (Di Vaio et al., 2012) and field-grown trees (Naor et al., 2013).

The daily dynamics of g_s differs from daily variation in E_p. In south Spain $g_{s\text{-max}}$ are usually achieved at 08:00-09:00 GMT, whereas maximum E_p is achieved from 09:00 GMT to 15:00 GMT, depending on atmospheric conditions (Fernández et al., 2011a). This is because D_a, the main driving variable for E_p, increases in south Spain from early morning to late afternoon. Plants respond to increasing D_a by closing stomata, such that decreasing g_s counterbalances increasing D_a until late afternoon (Eq. 2, Fig. 3). This may explain results of Moreno et al. (1996), who measured maximum sap flow rates in trunks of mature 'Manzanilla' between 13:00 and 14:00 GMT. However, porometer measurements showed that stomatal closure began much earlier, at 10:00 GMT. Sap flow at night also occurs in olive, the rate depending on environmental water status and plant capacity for water storage capacitance (Moreno et al., 1996; Fernández et al., 2006b). This accounts for nocturnal water recovery, which occurs at great extent in olive (Fernández et al., 2008b).

The seasonal trends of E_p in olive follow similar patterns than those of the potential evapotranspiration (ET_o), i.e. maximum daily E_p values are recorded at mid-summer in most olive orchards of Mediterranean areas (Fernández et al., 2008a). But, as compared to the spring and the autumn, ET_o values increase more in mid-summer than E_p values, contributing to lower crop coefficient (K_c) values in July and August than before and after this mid-summer period of great atmospheric demand (Fernández et al., 2006b; Testi et al., 2006a). The seasonal dynamics of the water evaporated from the soil (E_s) also affects markedly the K_c values, contributing to the low K_c values at mid-summer (Testi et al., 2006a).

4.3.3. Root-to-shoot signalling

A great number of papers have been published on stomatal closure being mediated by chemical and hydraulic signals, which are generated in roots suffering from water deficit. These signals are transported via the xylem to the shoots, and may act before a decrease in Ψ_l occurs, thus regulating stomatal opening and shoot growth (Wilkinson and Davies, 2002; Chaves et al., 2010). Inorganic ions, hormones and ethylene are involved in root-to-shoot signalling (Wilkinson and Davies, 2002; Dodd et al., 2006). Roots in drying soil synthesize ABA, part of which is transported through the xylem vessels, enters the leaf and reaches the apoplast of guard cells, thus affecting stomatal opening (Zhang and Outlaw, 2001). The fundamentals behind this long-distance signalling mechanism are complex, and seem to depend on xylem sap pH (Wilkinson, 2004) as well as on leaf microclimate (Davies et al., 2001). However, the source of drought-induced ABA remains under debate. Some authors argue that stomata mostly respond to ABA generated in the leaf, rather than in roots (Wilkinson and Hartung, 2009; Lobet et al., 2013). Recently the response of stomata to soil drying seems to depend mostly on hydraulic signals rather than on chemical signals in olive, especially under saturating light and high evaporative demand (e.g., at midday, Diaz-Espejo et al., 2012; Rodriguez-Dominguez, 2013). Fernández et al. (2003) reported restricted E_p in trees under localized irrigation, but they were unable to discriminate between ABA-induced or hydraulic signal-induced in response to decreasing soil hydraulic conductivity.

4.3.4. Leaf hydraulics

As mentioned above, different plant organs may have different vulnerability to embolism. This phenomenon, known as vulnerability segmentation (Zimmermann, 1983; Tyree et al., 1993), has been observed in a variety of species (Martinez-Vilalta et al., 2002). When embolism occurring, stomatal closure can be influenced by hydraulic signals originated in different organs. In olive, estimations of leaf-specific conductivity (k_l), i.e. leaf hydraulic conductivity normalised to unit leaf area, have been performed from hydraulic conductivity measurements at the whole-plant level (Dichio et al., 2013). Actual k_l measurements in olive potted plants can be found in Torres-Ruiz et al. (2013b): g_s and k_l showed considerable reductions at Ψ_l < -1.5MPa, thus suggesting a correlation between leaf hydraulic functioning and stomatal behaviour. Ψ_l and k_l recovered faster than g_s during re-watering, indicating other factors (possibly ABA) were involved in stomata opening (Section 4.6). Results on vulnerability to embolism of the different organs also show the occurrence of hydraulic segmentation in olive, making leaves effective in reducing whole-plant transpiration and, hence, in avoiding the spread of embolism in other plant organs (Torres-Ruiz et al., 2013b).

4.4. Leaf photosynthesis

The daily course of net CO_2 assimilation rate (A) is similar to that of g_s, such that maximum A values are achieved early in the morning (08:00-09:00 GMT), whereas g_s limits A in the remaining part of the day (Moriana et al., 2002; Fernández et al. 2006b). Olive is a C_3 plant which, under non-limiting conditions, can reach maximum A of 25 μmol CO_2 m^{-2} s^{-1} (Moriana et al., 2002; Diaz-Espejo et al., 2006; Tognetti et al., 2007; Fernández et al., 2008b), a low values as compared with other fruit trees. However, under limiting conditions olive tree is able to maintain appreciable A. In olive saturation of A occurs at I_p = 1000-1200 μmol m^{-2} s^{-1} (Natali et al., 1991). The dynamics of leaf water relations at the onset and as drought stress progresses greatly affect A. Jorba et al. (1985) found that reducing RWC from 96% to 65% depressed A by 85% in olive. Ennajeh et al. (2006) have shown steep decrease in g_s and A, in leaves of 'Chemlali' and 'Meski', when RWC decreased from 75% to 60%. At 35% RWC, g_s and A were < 50 mmol m^{-2} s^{-1} and < 4 μmol m^{-2} s^{-1}, respectively. In 'Leccino' Larcher et al. (1981) observed a decrease in A when Ψ_l fell to -1.3 MPa, and 50% reduction in photosynthesis occurred at Ψ_l of –2.2 MPa. Detectable A at Ψ_l as low as -7.0 MPa (Dichio et al., 2005) and Ψ_{stem} of -8.0 MPa (Moriana et al., 2002) have been reported.

Leaf photosynthesis depends on diffusional and non-diffusional limitations. The first limitation is due to diffusional resistances in the gas phase of CO_2 transport pathway from ambient air to carboxylation sites: this relates with both g_s and mesophyll conductance (g_m). The second includes biochemical processes, namely carboxylation rate and photosynthesis efficiency, which greatly depends on photoinhibition in olive.

4.4.1. Diffusional limitations of photosynthesis

At the beginning of the olive growing period (Fig. 1) the available soil water is usually high and values of global solar radiation (R_s) and ET_o are low. Under these conditions of low-to-moderate water stress, any decrease in A is mainly due to diffusional limitations, imposed by leaf resistances to ambient CO_2 from reaching the chloroplast (Fig. 2). Later in the season, increased water deficit and changes in leaf biomechanical and biochemical traits modify diffusional limitations to photosynthesis. Soil water depletion may increase diffusional limitation due to stomatal closure. In addition, g_m usually decreases in summer, in both irrigated and non-irrigated trees, because of increasing T_a

and D_a. Diaz-Espejo et al. (2007) found in ‘Manzanilla’ a maximum g_m of 0.224 mol m^{-2} s^{-1} at T_l = 29.61 ºC, and g_m of 0.14 mol m^{-2} s^{-1} at T_l = 40 ºC. Perez-Martin et al. (2009) showed a decrease in both g_s and g_m when soil water deficit and D_a increased: water deficit actually affected g_s more than g_m. Centritto et al. (2003) had already noted of considering stress-induced depletion in g_m to avoid overestimation of biochemical limitations to photosynthesis in olive. Changes in A due to leaf development in olive growing under harsh summer conditions have been reported as due to leaf age increasing the number of mesophyll cells and chloroplasts, as well as in CO_2-uptake cell surface (Bosabalidis and Kofidis (2002). Marchi et al. (2007) also reported of photosynthetic capacity increasing as leaves approaching to full expansion: mesophyll thickness doubled from initial through final leaf developmental. Proietti et al. (2012) observed that current-season leaves had greater A levels than one-year-old leaves. Recently published evidence on the importance of anatomical traits in the limitation of CO_2 diffusion from substomatal cavities to chloroplasts shows that g_m is strongly correlated with chloroplast exposed surface to leaf area ratio and mesophyll cell wall thickness, t_{cw} (Tomás et al., 2013).

4.4.2. Non-diffusional limitations of photosynthesis

During summer most Mediterranean species, including olive, likely suffer from photoinhibition due to soil water deficit and increasing atmospheric demand (Centritto et al., 2003, 2005; Denaxa et al., 2012). As summarized in Bacelar et al. (2007b) and in Boussadia et al. (2008), water stress-induced stomatal closure limits carbon availability at carboxylation sites. Therefore, absorbed light energy largely exceeds its use in photochemistry, thus leading to an excess of excitation in photosystem II (PSII). Under severe water stress, electron transport rate and quenching of excitation energy in PSII antennae are likely unable in dissipating excess excitation energy, leading to photodamage of PSII and net loss in D1 protein in PSII reaction centres. Photoinhibition may explain the lack of correlation between g_s and A in severely stressed olive (Natali, et al., 1991; Angelopoulos et al., 1996). Photoinhibition curtails olive performance, irrespective of morphological and anatomical adjustments (see Section 3.3 for details). Water stress-induced effects on leaf photochemistry have been reported in Bongi et a1. (1994), Bacelar et al. (2007b), Sofo et al. (2008), and Boughlleb and Hajlaoui (2011).

Diaz-Espejo et al. (2006) showed the ability of olive to adjust the photosynthetic apparatus to changes in environmental conditions. After seeing that ‘Manzanilla’ leaves had higher photosynthetic capacity in April than in August, the authors speculated that leaves with an inherently high potential in *A* conflicts with the highly-demanding summer conditions, when stomatal closure strongly limits CO_2 uptake. Maximum carboxylation efficiency ($V_{c\text{-}max}$), maximum rate of electron transport at saturating irradiance (J_{max}), and the capacity for triose phosphate utilization (TPU) were determined. Photosynthesis was limited by TPU and seasonal decrease in $V_{c\text{-}max}$ compensated for the stomatal limitation to CO_2 fixation, as the soil water deficit increased. This enables leaves to operate near to the transition point between photosynthetic limitation due to ribulose-1,5-bisphosphate (RuBp) carboxylation capacity and RuBP regeneration capacity, thus resulting in almost constant internal CO_2 concentration from April to August. Main model parameters, $V_{c\text{-}max}$, TPU, J_{max} and R_d (the rate of CO_2 evolution in the light resulting from processes other than photorespiration) were markedly influenced by T_l. Further, $V_{c\text{-}max}$ was positively correlated with leaf nitrogen content on area basis (N_a) and with SLW. Diaz-Espejo et al. (2007) worked with mature 'Manzanilla' trees under dry-farming conditions. In the spring the authors observed a positive relationship between V_{cmax} and N_a and daily integrated quantum flux density (Q_{int}). This, however, was not observed in summer. The authors hypothesized that this was due to stomatal limitations during summer, but also to a V_{cmax} down-regulation affected by g_m.

Bacelar et al (2007b) reported that the decline in daily *A* was largely due to stomatal limitations. However, C_i/C_a ratio increased markedly from morning to midday in non-irrigated plants, in spite of lower g_s, suggesting that non-stomatal limitations of photosynthesis prevailed under severe stress. Perturbations at chloroplastic level in rain-fed plants followed depression in maximum photochemical efficiency of photosystem II in the afternoon. Chlorophyll fluorescence measurements also revealed the occurrence of dynamic photoinhibition in irrigated trees. Boughlleb and Hajlaoui (2011) reported that water stress caused a marked decline on photosynthetic capacity and chlorophyll fluorescence in 'Chemlali' and 'Zalmati'. As water stress developed, *A*, g_s, E_p, the maximal photochemical efficiency of PSII (F_v/F_m) and the intrinsic efficiency of open PSII reaction centres (F'_v/F'_m) decreased. Proietti et al. (2012) observed lower *A* at the end of July than before and after, and shared the thesis that the low olive *A* values in the summer are due to damage of the photosystem induced by high temperature and drought stress, rather than to the lower g_s.

FIGURE 7 about here

4.4.3. WUE and water productivity

The plant water use efficiency (WUE) is evaluated from long-term measurements of cumulated dry matter and consumed water. When instantaneous gas exchange measurements are used, intrinsic water use efficiency (WUE_i) is estimated, i.e. the rate of carbon assimilated per unit leaf area per unit time and per unit water cost. Values of WUE_i in olive have been reported by Angelopoulos et al. (1996), Moriana et al. (2002) and Diaz-Espejo et al. (2006). Olive uses water more efficiently than other fruit trees. Bongi and Palliotti (1994) calculated that in southern Mediterranean area, the number of grams of fruit dry matter per kilogram of consumed water was 3.17 for olive, 2.46 for *Citrus*, and 1.78 for *Prunus*. Xiloyannis et al. (1996) reported WUE values (g CO_2 kg H_2O^{-1}) between 5.5 and 9.6 for olive, between 3.2 and 4.4 for grape, and between 2.3 and 3.5 for peach.

Although linear A vs. g_s relationships have been reported for olive (Chartzoulakis et al., 1999: Moriana et al., 2002; Boughalleb and Hajlaoui, 2011), A is affected later than g_s under water stress. Figure 7 shows A vs. g_s values collected in different Spanish- Italian locations and different cultivars (Fernández et al., 2008b). Constant A is estimated for decreasing g_s, until $g_s \approx 0.25$ mol m^{-2} s^{-1}. This is a key trait for the adaptation of olive to drought, and explains usually greater WUE_i recorded in plants under rain-fed than in irrigated conditions.

For agricultural purposes, achieving maximum WUE values is not necessarily the best option. Rather than WUE, most growers look at water productivity (WP). Water productivity as defined by Kijne et al. (2003) is the ratio of the amount of marketable product (per hectare) to unit of supplied water. In other words, WP is the net income per unit water used. A properly chosen irrigation strategy must increase both WP and the productive life of the orchard. Water productivity values, both for fresh fruits and oil, have been reported for different olive orchards (Table 1). Relationships between fruit yield and oil yield, and water consumed by the crop, have also been reported (Table 2). As expected, Tables 1 and 2 shows significant differences on WP depending on the cultivar, water regime and plant density. Additional details are given in Section 6.2.1. Other interesting relationships related to crop performance, such as the yield:LA ratio have been reported by Caruso et al. (2013), Proietti et al. (2012) and Fernández et al. (2013).

TABLE 1 about here

TABLE 2 about here

4.5. Response to re-watering

After a period of drought, root water uptake in olive increases immediately after soil water is newly available (Fernández et al., 2001). The rapid water uptake can explain the quick recovery in Ψ_l observed in olive after re-watering. The rate in Ψ_l recovery depends on the severity of previous water stress. Recovery may last few hours up to 4 days for plants with Ψ_l = -8.0 MPa at stress (Fereres et al., 1996; Fernández et al., 1997; Perez-Martin et al., 2011). Moreno et al. (1996) performed a recovery experiment with 25-year-old 'Manzanilla', by supplying water on September 12 to plants under dry-farming conditions over the whole summer. Both Ψ_l and E_p only partially recovered: sap flow measurements in main roots showed a significant increase in water uptake, but water flow was not detected in the outer sapwood annuli. This means that hydraulic root capacity did not fully recover, possibly due to cavitation of vessels.

In olive, gas exchange takes longer to recover than plant water status. As compared with Ψ_l, the delay in g_s and A recovery depends on the severity of the suffered water stress. Fernández et al. (1997) reported full recovery in g_s over two days re-watering in plants displaying Ψ_l = -4.2 MPa at midday. In the experiment by Fereres et al. (1996), on which trees reached midday Ψ_l = -8.0 MPa, g_s took several weeks to recover. The amount of water supplied during the recovery phase also conditions the speed of variables coming back to normal values (Fernández et al., 2013). Torres-Ruiz et al. (2013a) did not find a correlation between leaf hydraulic functioning and stomatal behaviour during recovery. They suggested that, similarly to that found in grape by Lovisolo et al. (2008), ABA accumulated in roots during drought was delivered to the rehydrated leaves, contributing to the slow g_s recovery. ABA-induced control in water transpiration may promote gradual embolism repair (Lovisolo et al., 2008).

5. Improving crop performance and management

In this section we address how new knowledge on the response mechanisms adopted by olive to cope with the environmental constraints imposed by the Mediterranean climate are currently used to both improve crop management practices and design more sustainable and productive crop systems. First we give an overview of models that have been developed to simulate key processes of olive performance. Examples on the use of modelling exercises as valuable tools to optimize orchard design and management are included. Then we summarize main knowledge for the effect of water and salinity on tree development and production. Then we consider new crop management practices for improving production and quality, as well as for increasing the sustainability of olive orchards, even in global change scenario.

5.1. Modelling

Moreno et al. (1996) used a transpiration model based on Penman–Monteith (P-M) equation to get reliable results for olive, after evaluating the fractions of sunlit and shaded leaves in the canopy. Mariscal et al. (2000a) formulated and evaluated a model to estimate PAR interception by olive orchards, at both instantaneous and daily levels. Leaf reflectance and transmittance, as well as the distribution of leaf inclination derived from field measurements were included in the model for reliable predictions of diffuse and total transmittance. Additional aspects related to radiation use efficiency (RUE) and dry matter partitioning were modelled by Mariscal et al. *(*2000b). Moriana et al. (2002) evaluated, for 'Picual' trees, the models of leaf conductance proposed by Jarvis (1976) and Leuning (1995). In addition, they proposed a third model to include the effect of water deficit into the Leuning's model. Diaz-Espejo et al. (2006) evaluated a photosynthesis model for 'Manzanilla' trees. They linked the photosynthesis model of Farquhar et al. (1980) with the model of stomatal conductance of Jarvis (1976), in which an effect of soil water deficit was included. Fernández et al. (2008b) used the model of Diaz-Espejo et al. (2006), together with the RATP model, to simulate daily values of E_p and A for olive trees with different leaf area density and canopy shapes. The RATP model was developed by Sinoquet et al. (2001) to simulate radiation transfer through the canopy of fruit trees. Marchi et al. (2007) built a model to simulate the rate of leaf development rate. The model allows simulate the import and export of carbohydrates, i.e. the sink-source balance in growing leaves. Authors estimated that the onset of carbohydrate export from olive leaves occurred at 28-29 days from leaf emergence. Diaz-Espejo et al. (2012) used the mechanistic BMF model of Buckley et al. (2003) to improve our understanding of the effect of limiting environmental conditions on the transpiration of drip irrigated olive trees.

Villalobos et al. (2000) used the P-M approach to build a model on ET_c for olive orchards. After combination with a modified version of the Ritchie's soil evaporation model (Bonachela et al., 1999), the model showed acceptable reliability and proved that the K_c approach can led to substantial errors due to local and temporal variations of main driving variables for transpiration, such as D_a. The effect of soil evaporation (E_s) on K_c estimations was further addressed by Testi et al. (2004), who used eddy covariance and water balance measurements in olive orchard to assess the relationships between orchard architecture and ET_c, under both dry and wet soil conditions. Testi et al. (2006b) used similar approaches to separate the two components of ET_c, and derived G_c values by inverting the P-M equation. Authors used the Jarvis model, calibrated for their orchard conditions, to improve the reliability of G_c. Villalobos et al. (2006) proposed a growth model for olive, based on the RUE concept. They showed that olive orchards have low RUE but compensate low RUE through high Harvest Index and large fraction of intercepted radiation. As a result, olive shows high oil productivity (ca. 3 t ha^{-1}) when compared to other oilseed crops. In addition, estimates of carbon sequestration by olive orchards showed a much larger potential for capture in olive than in other agricultural systems.

The model by Ritchie (1972) was used by Bonachela et al. (1999) to propose a soil evaporation model for rain-fed olive orchards. Bonachela et al. (2001) proposed a model for drip-irrigated orchards, which considered separately E_s in dry and wet ground areas. Lysimeter measurements were performed by Diaz-Espejo et al. (2008), who derived an improved model to estimate E_s in olive orchards. This allowed an accurate estimation of surface resistance (r_s) and E_s. Their results were unexpected, as cumulative E_s in drip-irrigated olive orchard were higher in ground areas with lower irradiance. Testi et al. (2006a) proposed a model of olive water requirements which estimates E_p and E_s separately. Values of K_c were calculated as the sum of three relevant coefficients related with tree transpiration (K_p), evaporation from the dry soil (K_{s1}) and evaporation from the areas wetted by the emitters (K_{s2}). The model offers the possibility of adding a fourth component, accounting for evaporation of the water intercepted by the canopy (K_{pd}). The model by Testi et al. (2006a) is a more mechanistic approach than that of the FAO crop coefficient method (Allen et al., 1998), since it takes into account main soil, weather and plant conditions.

5.2. Development and production as influenced by orchard conditions

5.2.1. Water

Soil water favours the number of fruits per tree, fruit f.w., fruit volume and pulp:stone ratio and, as a consequence, increases fruit and oil yields (Goldhamer et al., 1994; d'Andria et al., 2004; Gucci et al., 2007). It is known, however, that the water supplies needed to achieve the greatest WP values are usually below 100% ET_c. In fact, the relationships between water consumed by olive trees and both fruit and oil yield are curvilinear (Moriana et al., 2003; Grattan et al., 2006) (Table 2). This means that maximum potential production can be achieved with DI strategies. Reduced water supplies may have additional benefits in areas where local conditions lead to excessive vegetative growth, such as in northern Argentina (Correa-Tedesco et al., 2010; Searles et al., 2011). Deficit irrigation has greater impact on fresh fruit yield than on oil yield (Lavee et al., 2007). Fernández et al. (2013) carried out a 3-year study in an 'Arbequina' SHD olive orchard with trees under FI and two regulated deficit irrigation (RDI) strategies supplying 60% and 30% of the irrigation needs, IN (60RDI and 30RDI, respectively). Reductions in fruit and oil yields, as compared to FI, were 23% and 29% for 60RDI and 40% and 26% for 30RDI, respectively. Results for different olive cultivars are quite consistent in showing oil yield reductions of ca. 20% with ca. 50% DI strategies (Moriana et al., 2003; Iniesta et al., 2009; Caruso et al., 2013). The lower differences, between FI and DI trees in oil yield than in fruit yield, are partly due to the fact that irrigation increases the mesocarp water content, which penalizes physical oil extraction (Ramos and Santos, 2010; García et al., 2013; Gómez-del-Campo, 2013).

When the target is oil quality there are additional reasons for reducing irrigation. Results from experiments carried out in areas where the length of rainy season and average precipitation are high, have shown no clear effects of irrigation on oil quality (Tognetti et al., 2007; d'Andria et al., 2008). Most olive orchards, however, are in arid and semi-arid areas with dry seasons lasting for 5-6 months and average precipitation is lower than ~ 500 mm. Under these conditions, increasing irrigation s decreases total phenols content in olive oil and affect phenolic composition, resulting in oils of lower stability and poorer sensory attributes (d'Andria et al., 2004; Tovar et al., 2002; Servili et al., 2007; Machado et al., 2013). The bitterness, fruitiness and pungency are indeed less pronounced in oils from irrigated than from rain-fed trees (Stefanoudaki et al., 2009; Fernandes-Silva et al., 2013). Other attributes, such as colour, are also influenced by water supply (Pastor et al., 1998; Gómez-Rico et al., 2006, 2007; Servili et al., 2007). Grattan et al. (2006) and Berenguer et al. (2006) reported, for a SHD 'Arbequina' olive orchard, that production was maximized when irrigation water amounted to 70-75% of ET_c, but a sustained deficit irrigation (SDI) supplying 33-40% of ET_c resulted in excellent oil chemical parameters, flavour and stability. García et al. (2013) explored the impact of low-frequency deficit irrigation (LFDI) on the production and oil quality of 'Arbequina' olive trees. Severe water stress occurred between consecutive irrigation events causing leaf curling and fruit shrivelling. Oil quality is negatively affected when severe water stress episodes causing fruit shrivelling occurs near or at harvest time (Greven et al. 2009). García et al. (2013), however, found no negative effect on oil quality due to several periods of severe water stress. These findings support general believing that DI favours oil quality. However, physiological and productive responses under reduced irrigation depend on cultivar, local conditions and management practices (Tognetti et al. 2007, 2008; Fernández et al., 2008b; Ghandari et al., 2012). This may explain contrasting results in the pertinent literature (Dabbou et al., 2010; Tognetti et al., 2007; Stefanoudaki et al., 2009). Fatty acid composition was either unaffected (d'Andria et al., 2004, 2009; Motilva et al., 2000; Patumi et al., 2002) or affected (Berenguer et al., 2006; Gómez-Rico et al., 2007; Stefanoudaki et al., 2009) by irrigation treatments.

Other factors significantly influencing oil quality are harvesting date and fruit load. Dag et al. (2011) observed contrasting effects of harvesting date on the amount and quality of oil produced by 'Barnea' and 'Souri'. 'Barnea' required late harvest and advanced fruit maturity to get the maximum amount of good quality oil. In 'Souri', however, late harvest and advanced maturation caused an increase in fatty acids combined with a decline in polyphenol content resulting in loss of oil quality. García et al. (2013) reported that a late harvesting in 'Arbequina' led to loss of sensory quality and lower tocopherol content. In areas with early frosts it is recommended to harvest when the amount of oil expressed as % d.w. peaks (Gracia et al., 2012). The impact of water stress on yield and quality increases with crop load (Martín-Vertedor et al., 2011a; Naor et al., 2013). Concerning the harvesting method, handpicking is advantageous to improved oil quality, as compared to mechanical harvesting (Dag et al., 2008).

5.2.2. Nutrients

The response of olive to nutrient supplies has been addressed by Bongi and Palliotti (1994), Connor and Fereres (2005) and Sanzani et al. (2012). Here we just want to address the N fertilization, which is too often made incorrectly in olive orchards, and that of K, B and Fe, key elements for a correct olive fertilization.

The effect of N fertilization on growth, yield and oil accumulation in rain-fed 'Picual' olive trees was addressed by Fernández-Escobar et al. (2009, 2012). They concluded that annual applications of N are not needed in olive orchards growing in fertile soils, thanks to N mineralization of soil organic matter and the N supplied by rainwater. Rather, N must be applied only when the previous season's leaf analysis indicates that leaf N concentration is below the standard deficiency threshold, i.e. 1.4% of N in dried leaf. Reduced N fertilization was also recommended by Rodrigues et al. (2012), who made an above-ground balance of the nutrients removed by 'Cobrançosa' trees in a rain-fed orchard with 204 trees ha^{-1} and average fruit yield of 2500 kg ha^{-1}. They reported that 15-18 kg N ha^{-1} year^{-1} was adequate to balance the N annually exported. Morales-Sillero et al. (2007) fertigated 'Manzanilla' trees with a 4N-1P-3K fertilizer and three treatments supplying 200, 400 and 600 g N tree^{-1} year^{-1}, respectively. Fertilizing with 400 g N tree^{-1} year^{-1} led to the best equilibrium among oil quality, fertilization costs and environmental impact. The treatment supplying 600 g N tree^{-1} year^{-1} was considered the best for table olive production, since increased fruit size. This amount, however, was found to increase the risk for groundwater contamination (Morales-Sillero et al., 2009).

Potassium is a key element in the fertilization of olive orchards. Its concentration in the fruit is highly correlated with oil accumulation (Deidda, 1968). Potassium starvation has been reported to reduce shoot growth and WUE in 'Chemlali de Sfax' olive cuttings (Arquero et al., 2006). Moderate K deficiency impaired the plant's ability to regulate stomatal closure, so g_s increased. This effect was more evident in water-stressed plants than in FI plants. Although results on B application in olive are controversial, it seems that B deficiency affects negatively fruit set and development (Perica et al., 2001), and that foliar B applications have positive effects on blooming rate and yield, especially on years of low fruit set (Larbi et al., 2011). Foliar application of B, therefore, may be advisable in 'off' years following a year of high production. Another important element for olive fertilization is Fe, especially for trees growing in calcareous soils. Iron chelates are widely used, but they are expensive and can be easily lost by leaching. Poorly soluble, slow-release Fe fertilizers such as synthetic siderite ($FeCO_3$) are effective on preventing Fe chlorosis in 'Picual', 'Picudo' and Lechín de Sevilla' trees (Sánchez-Alcalá et al., 2012). Olive trees fertilized with $FeCO_3$ showed greater leaf chlorophyll concentration, as well as greater yields, although the effect on yield was significant in 'Picual' trees only.

5.2.3. Salinity

The response of the olive tree to both salty soils and irrigation with saline water has been widely studied, likely because of high number of olive orchards being affected by salinity. Details have been summarized in several review papers (Bongi and Pallioti, 1994; Gucci and Tattini, 1997; Chartzoulakis, 2005; Ben-Gal, 2011; Sanzani et al., 2012). Olive is considered to have a moderate-to-high tolerance to the presence of salts in the soil (Tattini et al., 1995). Crop performance decreases when water for irrigation has an EC greater than 5.5 dS m^{-1} (Freeman et al., 1994), and the limit of salt content in irrigation water for is 8 g L^{-1} of solid residue (Zarrouk and Cherif, 1981). Positive effects of salinity on oil quality have been reported for irrigation at EC > 7.5 dS m^{-1} (Ben-Gal, 2011). For the sodium adsorption ratio (SAR), values lower than 9 do not affect production (Freeman et al., 1994), and a SAR value of 26 has been observed to be tolerated by mature olive trees (Loreti and Natali, 1981).

A balanced presence of salts in the rhizosphere is required for plant growth, but high concentrations of soluble salts in the rhizosphere lower Ψ_s. The energy required to take up water then increases (Eq. 1, Fig. 3), such that growth and production markedly decrease. In extreme cases, plant cannot compete for water vs. the soil and dies due to dehydration. Most often, salt-induced decrease in Ψ_s just increases water stress in the tree, such that salt stress depresses Ψ_l, RWC (Gucci et al., 1997) and g_s (Tattini et al., 1995). It is not surprising, therefore, that A is reduced with increasing salinity in olive (Bongi and Loreto, 1989; Tattini et al. 1997; Loreto et al., 2003; Chartzoulakis et al., 2002; Chartzoulakis 2005). Detailed experiments on the effect of irrigating several Greek cultivars with salty water were conducted by Centritto et al. (2003) and Loreto et al. (2003). They show that salt stress affected g_s and g_m but not the biochemical capacity to assimilate CO_2. Salt-induced reductions in A were mostly driven by low g_s and g_m.

Toxicity by specific ions can also affect olive growing in saline environments. Na^+ and Cl^-, toxicity occurs when concentrations in leaves sampled in July are greater than 0.2% and 0.5%, respectively (López-Villalta, 1996). Olive is able to avoid ion toxicity by salt exclusion as well as by compartmentalization of specific ions. Plants retain greater concentrations of Na^+ and Cl^- in roots and basal parts of the trunk as compared with upper parts of the canopy (Tattini et al., 1992; Gucci and Tattini, 1997; Chartzoulakis, 2005). Salt exclusion by olive roots was reported by Benlloch et al. (1991) and Melgar et al. (2006). Reductions in growth and yield due to salinity have been widely reported (Gucci and

Tattini, 1997; Chartzolulakis et al., 2002; Chartzoulakis 2005; Bracci et al., 2008). Long-term studies with trees under field conditions by Aragües et al (2005) with 'Arbequina' trees show that above 4 dS m^{-1} EC, reductions in yield ranging from 16 to 23% per 1 dS m^{-1} occurred. In contrast, Melgar et al (2009a) did not find significant effects on plant performance of salinity in the range 0.5 - 10 dS m^{-1}. The response of the olive tree to salinity can change if combined with other environmental stresses, such as hypoxia (Aragües et al., 2004) and high solar irradiance (Remorini et al., 2009; Melgar et al. (2009b). Other examples of the salinity tolerance of olive trees when affected by other stresses are given by Cimato et al. (2010) and Ben-Gal (2011).

5.3. Water management

The increasing understanding of the response of olive to environmental stresses has allowed the development of water management practices which greatly contribute to the sustainability and productivity of olive orchards in areas with harsh conditions. Bellow we summarize those practices with a greater impact on the design and management of new olive orchards.

5.3.1. Deficit irrigation strategies

The effective adaptation of olive to stressing conditions confers it both a high capability for survival and a marked productive response to favourable conditions. This explains that ca. 22% of the ca. 10.5 Mha global area cultivated with olive is under irrigation (IOC www.internationaloliveoil.org). In Mediterranean regions with mean annual ET_o and precipitation values of ca. 1200 mm and ca. 500 mm, respectively, mature drip-irrigated olive orchards with planting densities from 100 to 300 trees ha^{-1} require about 7000 m^3 ha^{-1} $year^{-1}$ to replace ET_c. Of these, between 3000 and 4000 m^3 ha^{-1} are the IN required for FI (Fernández and Moreno, 1999; Gucci et al., 2012a). For SHD olive orchards with plant densities close to 2000 trees ha^{-1}, IN may increase to 5000 m^3 ha^{-1} (Fernández et al., 2013). As mentioned in Section 4.4.3, however, acceptable WP values are achieved with irrigation amounts (IA) lower than IN, which explains the success of several DI strategies applied to olive orchards.

On the first years after planting IA must be similar to IN, for the orchard to establish as soon as possible. Later, a DI strategy is usually the best option. When water for irrigation is really scarce, supplementary irrigation, also called complementary irrigation, could be the only suitable DI strategy. Despite of consisting of just one or very few irrigation events, it can lead to substantial increases in crop performance (Lavee et al., 1990; Proietti et al., 2012). Greater IA are supplied with LFDI (Lavee and Wodner, 1991), SDI (Goldhamer et al., 1994), and RDI (Goldhamer, 1999). A comparison study between SDI and LFDI in an 'Arbequina' orchard with led to no differences on main variables related to oil production and quality were (García et al., 2013). Both SDI and RDI are being widely used in olive orchards (Moriana et al., 2003; Iniesta et al., 2009; Ramos and Santos, 2009). With SDI a fixed fraction of IN is supplied all throughout the irrigation season. With RDI water supplies are equal or close to IN in the phases of the growing cycle when the crop is more sensitive to water stress, and are markedly reduced for the rest of the cycle (Chalmers et al., 1981). Significant water savings are achieved with both strategies, with little impact on yield and marked improvements in oil quality (Fernández et al., 2013; García et al., 2013). As compared to FI, SDI is particularly interesting in the 'off' years, when the lower crop load makes the olive tree less sensitive to water deficit (Martín-Vertedor et al., 2011a,b).

Both tree density and root zone size condition the choice of the DI strategy. SDI seems to be particularly interesting when the trees explore large soil volumes, i.e. in orchards with medium to low densities and deep soils (Moriana et al., 2003; Iniesta et al., 2009; Ramos and Santos, 2010; Fernandes-Silva, 2010). In these cases, the soil water stored during the rainy season may better compensate for the difference between IA and IN. The literature provides examples of olive orchards with 400 to 600 trees ha^{-1} under FI (Testi et al., 2006a; Pastor et al., 2007), SDI (Gucci et al., 2012b) and RDI conditions (Patumi et al., 2002; d'Andria et al., 2004). Grattan et al. (2006) and Berenguer et al. (2006) explored the convenience of applying SDI with different levels of irrigation reduction in a SHD olive orchard in California. In these orchards, however, the reduced root zone makes RDI more advisable than SDI, to limit the risk of excessive water depletion on the most sensitive phenological stages. Examples of the application of RDI to SHD olive orchards have been published by Gómez-del-Campo (2010, 2013) and Fernández et al. (2013) (Fig. 8). When applied to SHD olive orchards, DI strategies can be adequate not only to increase WP, but also to avoid problems derived from excessive vigour (Connor, 2006; León et al., 2007) and to improve oil quality (Section 6.2.1).

The partial root zone drying (PRD), first developed in Australia for vineyards, is a DI strategy which relies on root-to-leaf signalling (Dry et al., 1996). When a fraction of the root system remains in drying soil while the rest are kept well watered, a root-to-leaf signalling mechanism is triggered, reducing stomatal aperture and leaf growth, preventing water loss (Dry et al., 2001; Dodd et al., 2006). The wet portion of the root system maintains a favourable plant water status such that yield is not compromised and quality may improve (Dry et al., 2001). Wahbi et al. (2005) and Centritto et al. (2005) analysed the effect of applying PRD (50% of ET_c) to 'Picholine marocaine' olive trees. Wahbi et al. (2005) reported a yield reduction of 15-20% only, and no reduction in yield quality, as compared to control trees irrigated in both sides to 100% of ET_c. Centritto et al. (2005) found a significant decrease in Ψ_l measured in the PRD trees as compared to the FI trees, although values of leaf RWC and A were similar. Unfortunately, they did not have a companion RDI treatment. Fernández et al. (2006b) compared a PRD and a RDI treatment, both supplying 50% of IN, in a 'Manzanilla' orchard, and found no differences on water status, gas exchange and sap flow. In mature trees with localized irrigation roots are under a wide range of soil water conditions, from well watered roots within the irrigation bulbs to roots in dry soil far away from the bulbs and roots in the interface between the wet bulbs and dry soil volumes, which have an intermediate water status. It seems that, in those cases, there is no need to alternate irrigation for a root-to-shoot signalling mechanism to occur.

FIGURE 8 about here

5.3.2. New methods for scheduling irrigation

Reliable monitoring of tree water stress is required for a correct management of any DI strategy. This applies mainly to RDI, since the occurrence of severe water stress episodes on sensitive phases of the growing period must be avoided (Fig. 8) to minimize the risk of reducing both the current year yield and the productive life of the orchard (Fernández et al., 2013). New water stress monitoring methods are being developed from the increase on knowledge on crop physiology and improvements on monitoring and data transmission systems. Most of these methods are based on plant measurements (Fig. 9), including sap flow (SF) and trunk diameter variation (TDV) measurements (Fernández and Cuevas, 2010; Ortuño et al., 2010). Conventional indicators such as Ψ_{stem} are also reliable and can be used for an effective control of irrigation in olive orchards (Moriana et al., 2012; Naor et al., 2013). Those indicators, however, do not have the advantages derived from automatic and continuous recording and data transmission and storage systems of the new methods. The works by Fernández et al. (2008c), Ramos and Santos (2009) and Rousseaux et al. (2009) with SF measurements and those by Pérez-López et al. (2008), Moriana et al. (2010) and Cuevas et al. (2010) with TDV measurements show the potential and limitations of both methods for monitoring water stress and scheduling irrigation in olive orchards. Fernández et al. (2011a) used concomitant SF and TDV measurements to assess water needs in a mature 'Manzanilla' olive orchard. Their results, together with those reported by Fernández et al. (2011b) and Cuevas et al. (2013) show that the daily difference, both for tree water consumption ($D_{E\mathrm{p}}$) and maximum trunk diameter (D_{MXTD}), between deficit irrigated trees and trees growing under non-limiting soil water conditions were reliable indicators of the onset and severity of water stress.

The leaf patch clamp pressure probe, or ZIM probe (Zimmermann et al., 2008) is a relatively new device able to record automatically and continuously the so called leaf patch output pressure (P_{p}), which is inversely correlated with the leaf turgor pressure, P_{c} (> ca. 50 kPa), a variables closely related to Ψ_{l} and g_{s} (Ache et al., 2010). The ZIM probe have been tested in olive by Ben-Gal et al. (2010), Fernández et al. (2011b), Ehrenberger et al. (2012) and Rodriguez-Dominguez et al. (2012). Results show that this is a promising method to monitor water stress and to schedule irrigation. Other plant-based method with a potential for scheduling irrigation in olive is that based on measurements of stem electrical conductivity with TDR probes (Nadler et al., 2008), although this method is less popular than the previously mentioned.

When combined with aerial or satellite imaging, the reported methods can be used for precise irrigation in large orchards with high crop-water-stress variability. An example on drought-induced changes in the spectral reflectance of olive leaves was given by Sun et al. (2008). Examples on the use of field measurements in olive orchards combined with airborne images are given in Zarco-Tejada et al. (2009) and Berni et al. (2009). Results showed that combining airborne imagery with automated records of plant water stress is a promising approach for monitoring water stress in large commercial olive orchards. Thermal images of individual trees, such as those taken from a crane about 15 m above the canopy by Ben-Gal et al. (2009), also shows a potential to schedule irrigation, although difficulties arise form the need of normalizing the canopy temperature to remove the effect of environmental conditions.

FIGURE 9 about here

5.4. Facing global change

Climate scenarios foresee significant changes in atmospheric conditions of main olive growing areas. The atmospheric demand is expected to increase, the rainfall to decrease, and the concentration of several gases in the air, such as sulphur dioxide (SO_2), tropospheric ozone (O_3) and carbon dioxide (CO_2) to increase. In addition, the quality of the incoming radiation is expected to change, with a possible increase in solar ultraviolet radiation (Sebastiani et al., 2002). These changes can affect olive productivity. In a work by Giorgelli et al. (1994), ‘Frantoio’ and ‘Moraiolo’ olive plants were exposed to increasing [SO_2] (0, 35, 70 and 100 ppb). After five months, ‘Frantoio’ plants showed decreasing A and g_s values with increasing [SO_2]. These effects were not observed in ‘Moraiolo’ plants. Stomatal density (S_D), stomatal opening and the percentage of transpiring surface decreased progressively with [SO_2], especially in ‘Frantoio’ but also in ‘Moraiolo’ plants. Minocci et al. (1999) studied the effect of O_3 concentrations on the leaf physiology and morphology of both cultivars. Both g_s and A decreased significantly in plants exposed to [O_3] = 100 ppb, as compared to those exposed to [O_3] < 3 ppb (control), especially for ‘Frantoio’. Leaves developed under high [O_3] showed greater S_D than leaves under natural, control conditions, but the actual transpiring stomatal surface decreased by ca. 50% in both cultivars. The authors concluded that this can led to significant O_3-induced reduction in olive productivity in areas where [O_3] is expected to increase. Also in ‘Frantoio’ and ‘Moraiolo’ plants, Tognetti et al. (2001) reported that exposure to elevated 560 μmol CO_2 mol^{-1} enhanced A and decreased g_s, leading to greater WUE$_i$ values. Stomatal density decreased with elevated [CO_2]. Differences in A were due to the stomata limitation and not to differences in the capacity of the photosynthetic apparatus. Additional details on the effects of air pollutants in the olive tree performance are given in the review paper by Sebastiani et al. (2002). They also reported main effects of enhanced UV-B radiation. The depletion of the ozone layer, a natural filter for UV-B radiation, is leading to increasing crop UV-B irradiance. The authors summarized a number of papers on the effect of UV-B radiation in olive, and outlined that the species shows high resistance to increased levels of UV-B, thanks to the protective effect of trichomes and to the synthesis of UV-B absorbing compounds at the leaf surface, such as flavonoids and anthocyanins.

Other air pollutants are particles from industrial activities. The effect of dust released from cement factories on olive leaf physiology was investigated by Nanos and Ilias (2007). Cement kiln dust applied to developing 'Knoservolea' olive leaves caused the chlrophyll a/chlorophyll b ratio to change and A to decrease. According to the authors, this could have been due to changes both on the amount and quality of the light reaching the chloroplasts. They also suggested a negative effect of the heavy metal toxicity of the dust on the photosynthetic apparatus.

The influence of climate change on the olive flowering phenology was evaluated, for Spanish and Italian cultivars, by García-Mozo et al. (2009). They reported that the olive flowering phenology will be more affected by the late spring temperature than by the winter or the early spring temperature, such thus that olive may be less affected by global warming than other early-spring-flowering species. Even so, Avolio et al. (2012) estimated that an advance of pollen season in Calabria (Italy) of about 9 days is expected for each degree of T_a rise. The authors estimated, from phenological model results and climate predictions, an anticipation of maximum olive flowering between 10 and 34 days, depending on the area. Tunahoğlu and Durdu (2012) evaluated the vulnerability of several Turkish olive cultivars to climate change. They reported that the expected increases in moisture deficit, average temperature and the frequency of extreme events in the Mediterranean Basin, will lead to significant decreases in olive oil yield. Recently, Orlandi et al. (2013) implemented a regional phenological model derived through the growing season index (GSI, developed for the prediction of plant phenology in response to climate). The authors demonstrated that the GSI-phenologial model for olive predicted its intra-annual dynamics throughout Mediterranean cultivation areas. With the help of the model and data on local climatic changes over the last two decades, the authors predicted the possibility of a northward shift of olive cultivation areas, due to the enlargement of the growing season in winter, as well as a failure to satisfy the minimum chilling requirements in traditional southern cultivation areas.

Caution must be taken when extrapolating the abovementioned results to other locations and conditions. Iglesias et al. (2010) evaluated the adaptation of several crops, including olive, to changing climate. Results for the same crop were highly variable depending on location. The authors concluded that not only crop-specific responses, but also location-specific responses, including management and socio-economic conditions, must be taken into account when assessing the effect of changing climate scenarios in agriculture.

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Fig. 1. Growing cycle of the olive tree in south Spain on a typical year. Shoot growth normally stops in July, although it may resume from late August. Fruit growth does not always show a double sigmoid curve as that depicted in the figure. Instead, a rather constant fruit growth rate is often observed, all throughout the summer, especially in fully irrigated trees. HS1 to 3 = periods of high sensitivity to water stress. WAB = weeks after bloom.

Fig. 2. Cross sections of the upper, or adaxial (A), and lower, or abaxial (B), surfaces of an olive leaf. The conductances of the boundary layer (g_b), stomata (g_s) and mesophyll (g_m), related to changes from the CO_2 concentration in the surrounding air (C_a) to that in the chloroplast (C_c), are depicted. The CO_2 concentrations next to the stomata (C_s) and in the intercellular air spaces within the leaf (C_i) are also represented. The photos show chloroplast within cells both of the palisade parenchyma (left) and spongy mesophyll (right). Photos by Dr. A. Diaz-Espejo. After Flexas et al. (2008).

Fig. 3. Main functional and physiological traits of the olive tree related to its adaptation to drought. Equations 1 and 2 relate main variables related to tree transpiration (E_p). Ψ_s = effective soil water potential; Ψ_l = effective leaf water potential; Ψ_x = xylem water potential; R_p = plant hydraulic resistance; G_c = canopy conductance; $D_{l\text{-}a}$ = leaf-to-air vapour pressure deficit; P = atmospheric pressure; g_s = stomatal conductance.

Fig. 4. Sap flow probes (Heat Field Deformation method) installed in roots of a ‘Cobrançosa’ olive tree to estimate ‘normal’ (from roots to leaves) and reverse flows. This was part of an experiment run by the team of Prof. M.I. Ferreira (ISA, University of Lisbon) with the collaboration of Prof. N. Nadezdhina (Mendel University, Brno), within the frame of the WUSSIAAME project coordinated by the ISA team. Photos taken by Prof. Ferreira at the experimental plot, in an olive orchard close to Beja (Portugal).

Fig. 5. Cryo-scanning electron microscope images of frozen-hydrated samples of current-year ‘Manzanilla’ olive shoots. On the left, a longitudinal freeze-fracture showing several pits along the xylem vessels. On the right, a transversal fracture of a single pit, showing the inner membrane. The samples were analysed by Dr. A. Minnocci, (Inst. of Life Sciences, Scuola Superiore Sant' Anna, Italy), in a Philips SEM 515 equipped with a SEM Cryo Unit SCU 020. The work was made within the frame of a Bilateral Agreement MIUR-CSIC

involving the author and Prof. L. Sebastiani (Inst. of Life Sciences, Scuola Superiore Sant' Anna, Italy).

Fig. 6. Xylem vulnerability curves built from samples of current-year shoots taken from mature ‘Manzanilla’ olive trees growing close to Seville, southwest Spain. Both rain-fed trees and fully irrigated trees were sampled. The curves show the percentage loss of hydraulic conductivity (PLC) as a function of decreasing xylem water potential (Ψ_x). Data points are the average of five to seven samples; vertical bars represent ± the standard error. The doted grey lines indicate the Ψ_x value associated with a 50% loss of hydraulic conductivity (P_{50}). Data represented in the figure were recomputed considering PLC = 0 at $\Psi_x = 0$, and the resulting vulnerability curve (in grey colour) fitted and plotted. The dashed line represents the tangent through the midpoint of the vulnerability curve and its x-intercept represents the air entry pressure (P_e) following Meinzer et al. (2009). After Torres-Ruiz et al. (2013a).

Fig. 7. Net CO_2 assimilation (A) versus stomatal conductance (g_s) values measured in five different olive cultivars, irrigated and non-irrigated, at four locations in Spain and Italy. Data points represent the average of single measurements averaged for 0.05 mol m^{-2} s^{-1} g_s intervals. After Fernández et al. (2008b).

Fig. 8. Regulated deficit irrigation strategy for hedgerow olive orchards with high plant densities. The three periods on which the irrigation needs (IN) are equal or close to the crop demand correspond to the three periods of high sensitivity to water stress depicted in Fig. 1. ET_c = crop evapotranspiration under non-limiting soil water conditions; P_{eff} = effective precipitation, or fraction of total precipitation that reaches the root zone; i.e. / w. = irrigation events per week; WAB = weeks after bloom. After Fernández et al. (2013).

Fig. 9. Plant-based methods used in olive trees to monitor water stress and to schedule irrigation: heat-pulse velocity probes for sap flow estimations (a), a leaf patch clamp pressure probe to estimate leaf turgor pressure (b), a radial dendrometer to record trunk diameter variations (c) and a time domain reflectrometry sensor to measure the trunk electrical conductivity (d).

Figure 1

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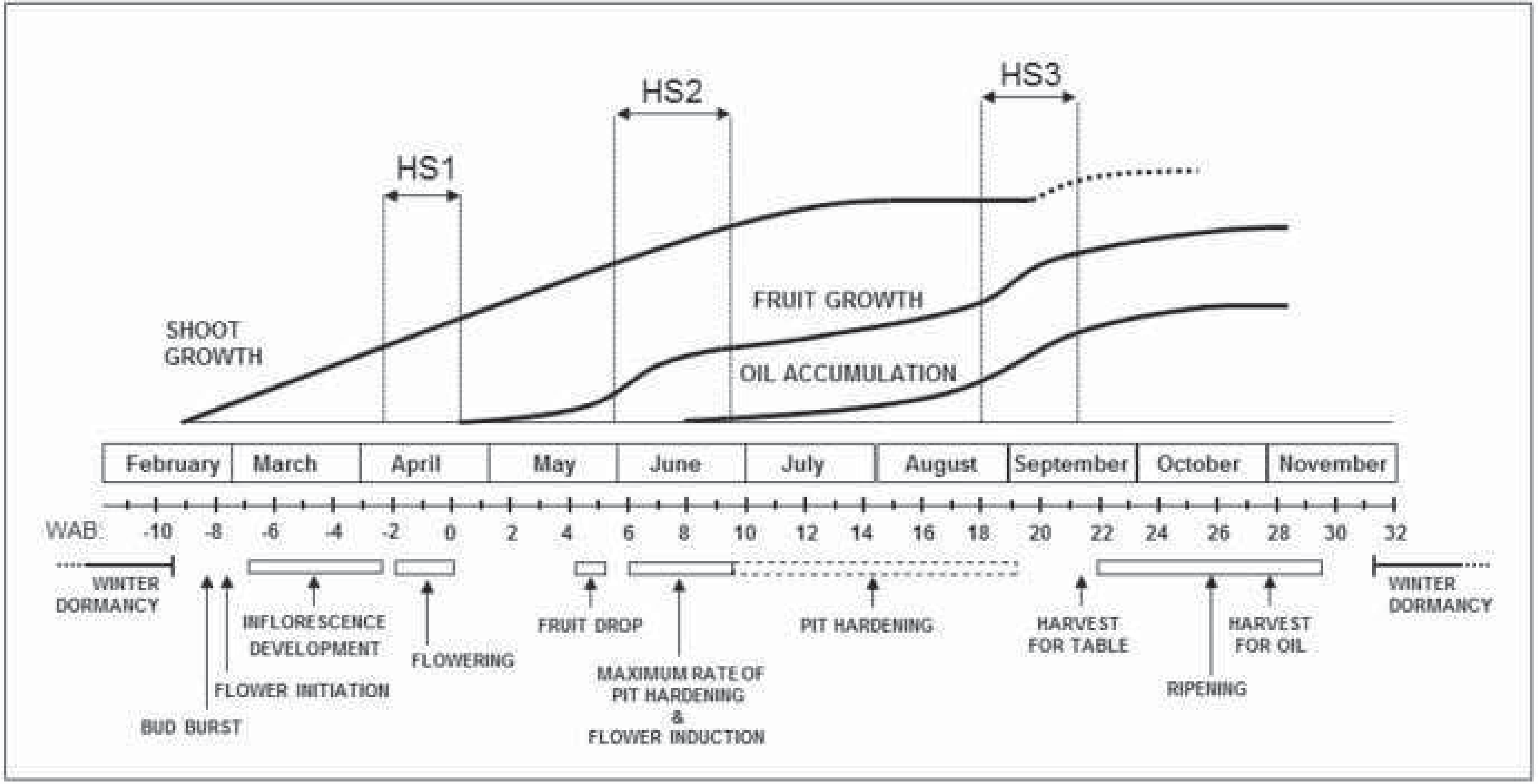

Figure 2
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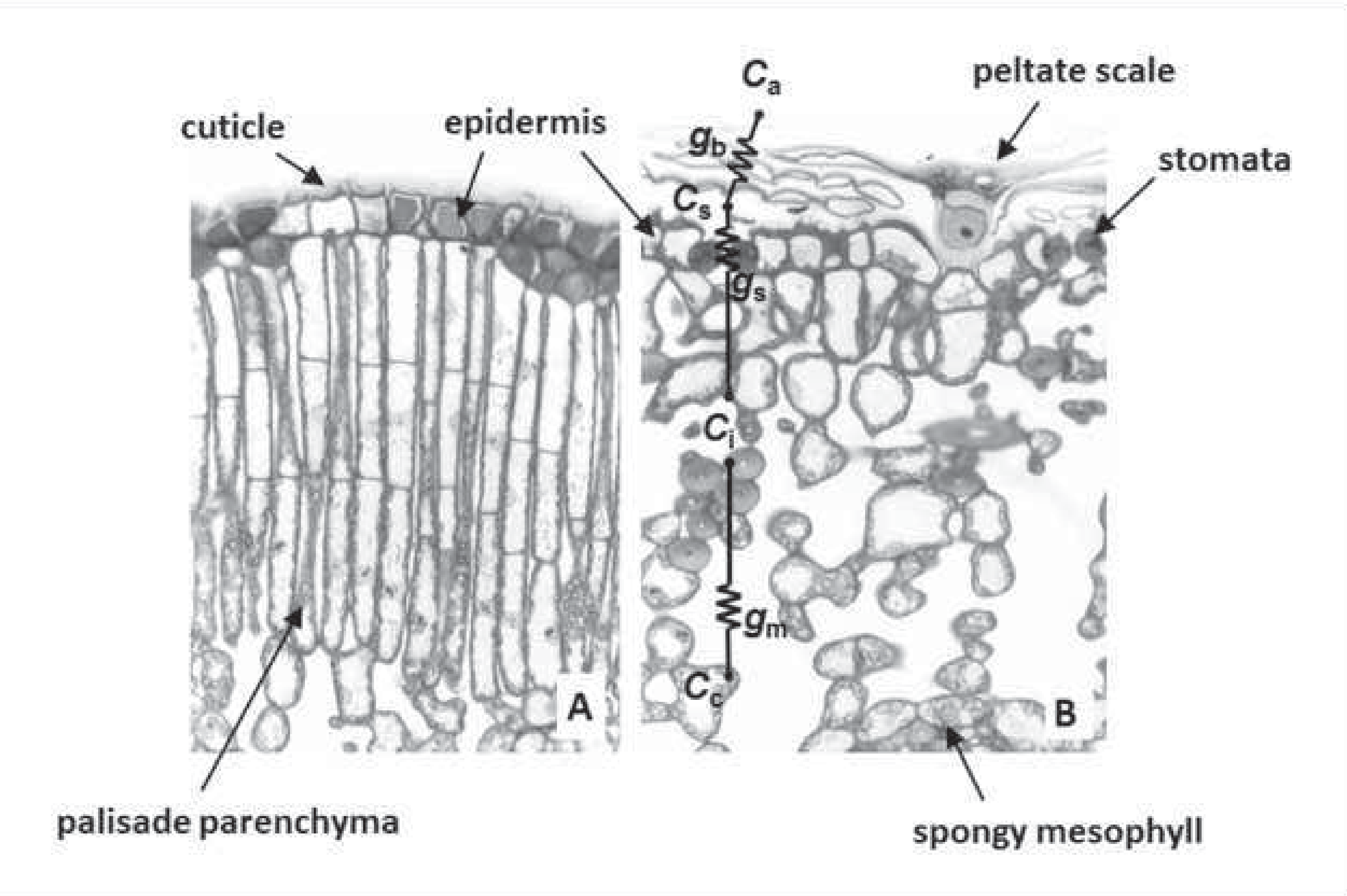

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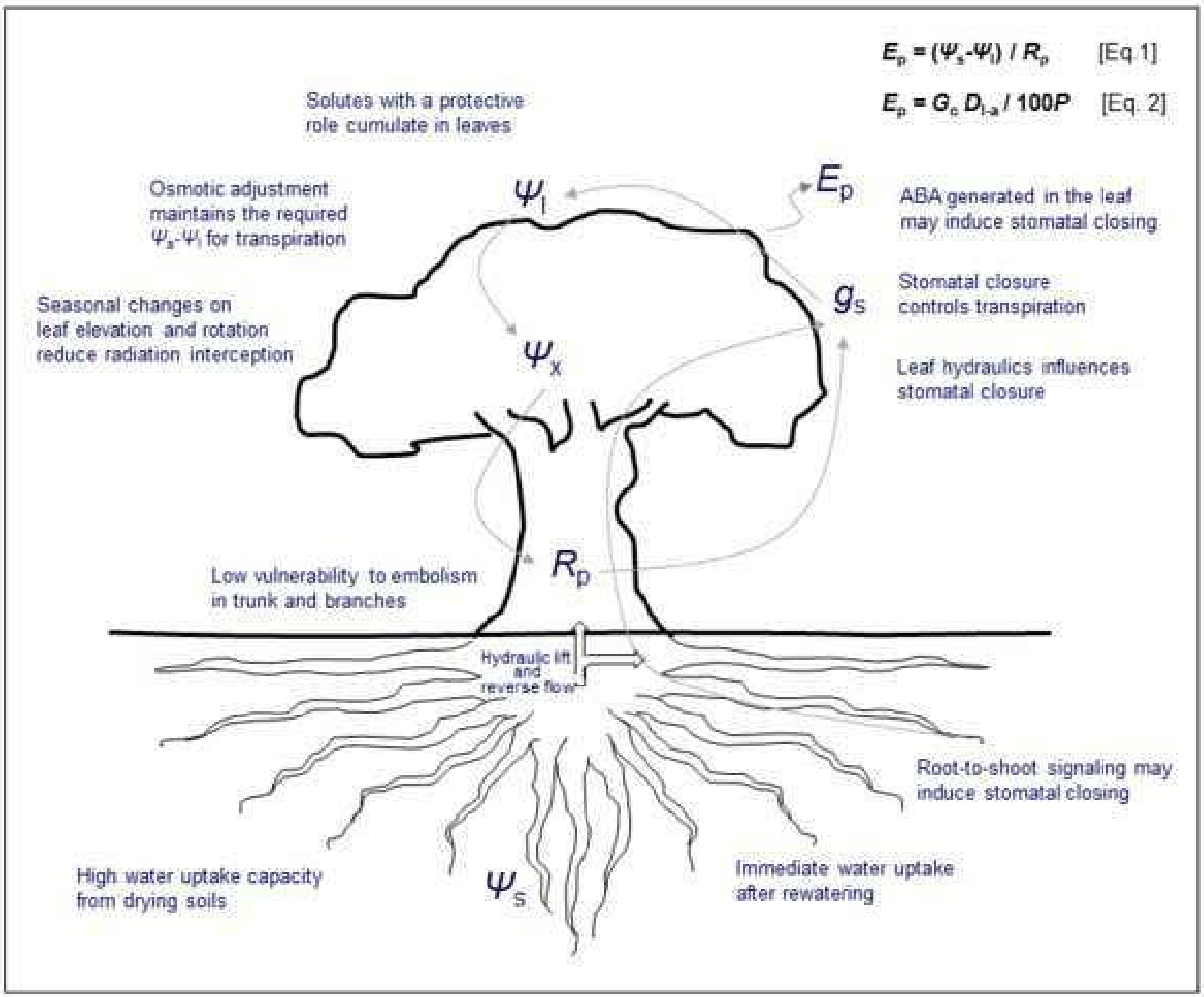

Figure 4

Figure 5

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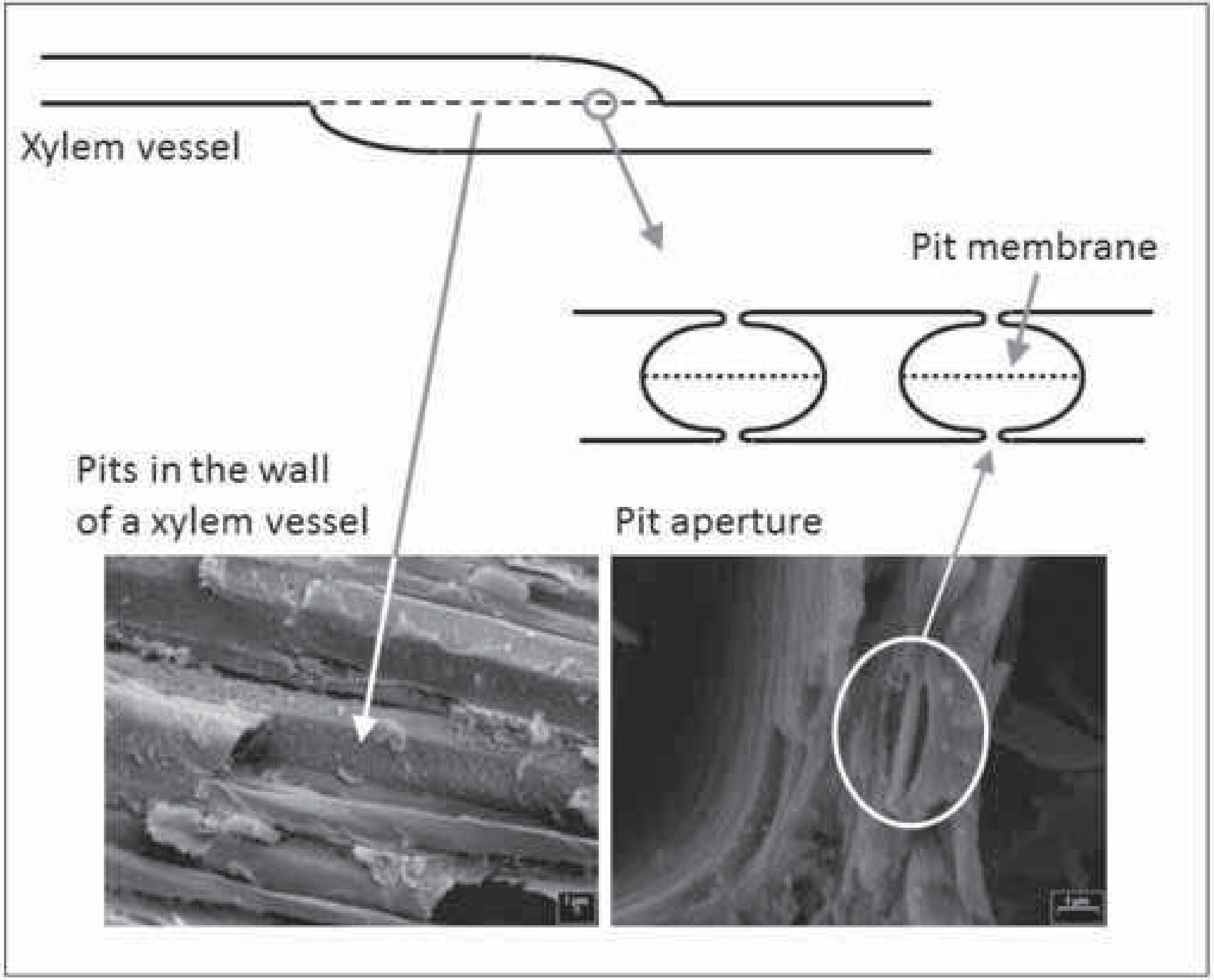

Figure 6

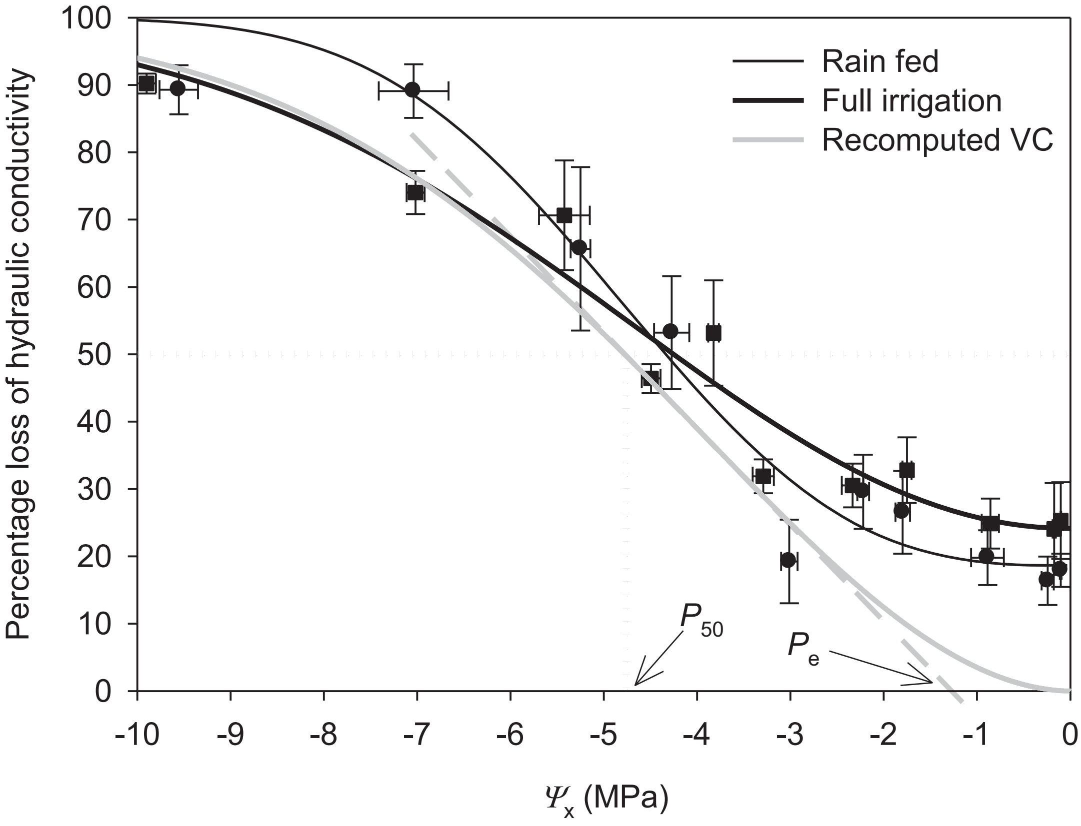
Percentage loss of hydraulic conductivity
100
90
80
70
60
50
40
30
20
10
0
-10
-9
-8
-7
-6
-5
-4
-3
-2
-1
0
Ψ_x (MPa)
Rain fed
Full irrigation
Recomputed VC
P_{50}
P_e

Figure 7

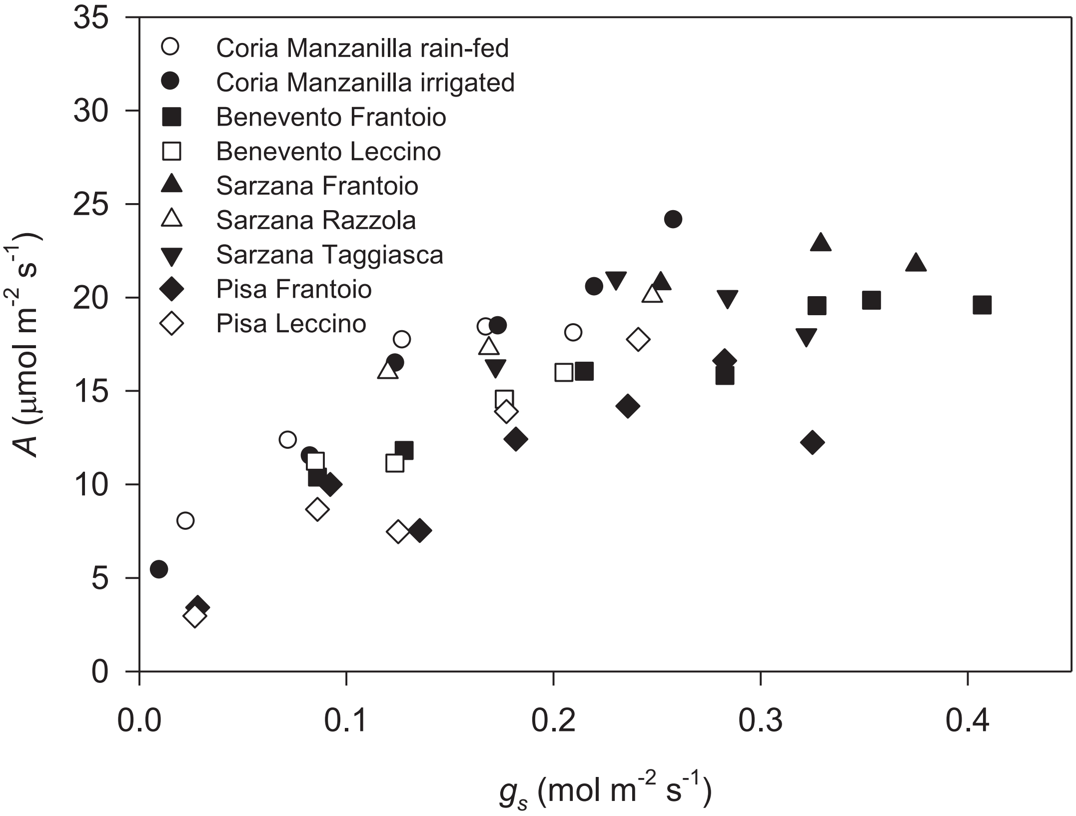
35
30
25
20
15
10
5
0
0.0
0.1
0.2
0.3
0.4
Coria Manzanilla rain-fed
Coria Manzanilla irrigated
Benevento Frantoio
Benevento Leccino
Sarzana Frantoio
Sarzana Razzola
Sarzana Taggiasca
Pisa Frantoio
Pisa Leccino
A (μmol m^{-2} s^{-1})
g_s (mol m^{-2} s^{-1})

Figure 8

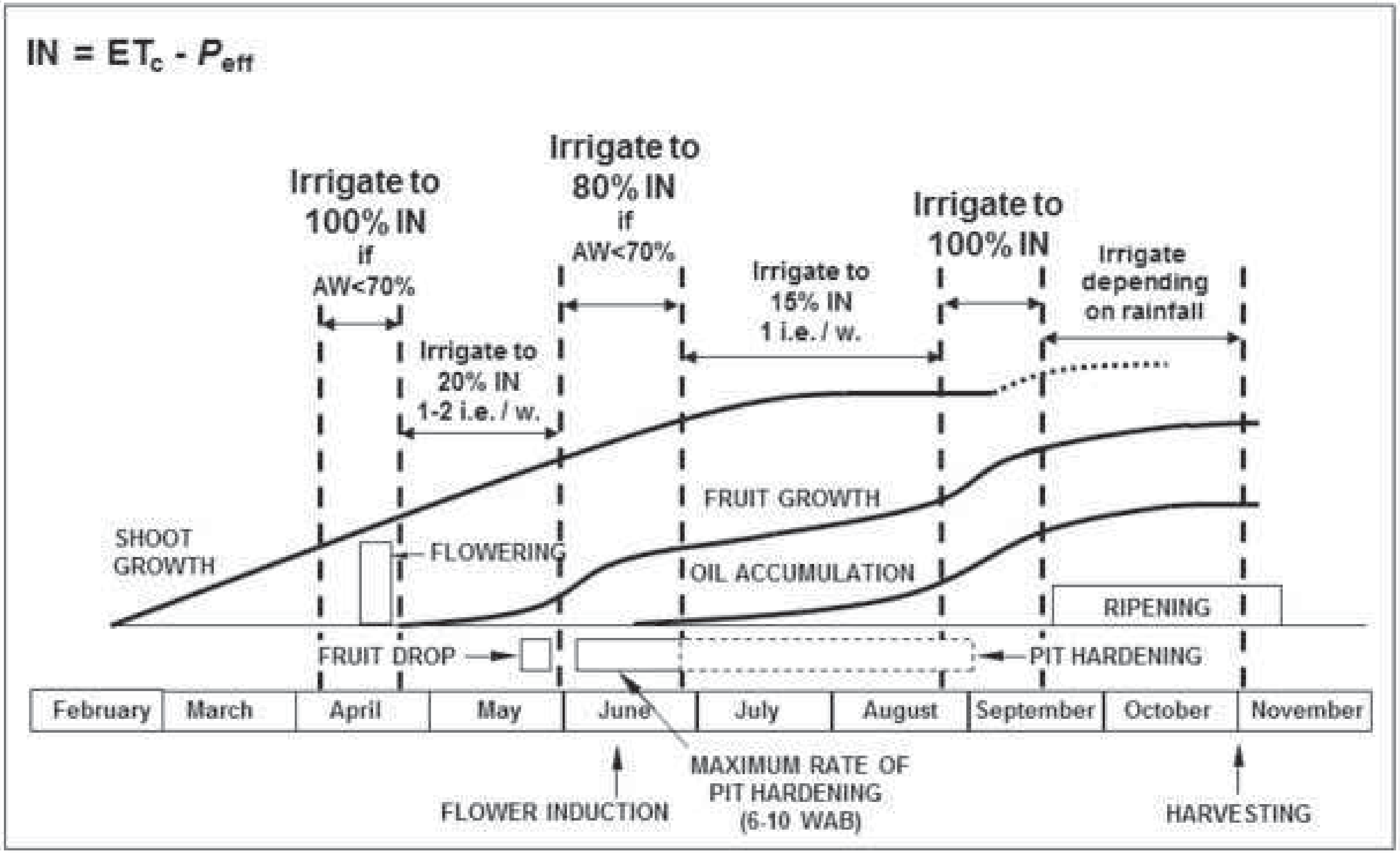
IN = ET$_c$ - P_{eff}
Irrigate to 100% IN if AW<70%
Irrigate to 20% IN 1-2 i.e. / w.
Irrigate to 80% IN if AW<70%
Irrigate to 15% IN 1 i.e. / w.
Irrigate to 100% IN
Irrigate depending on rainfall
SHOOT GROWTH
FLOWERING
FRUIT GROWTH
OIL ACCUMULATION
RIPENING
FRUIT DROP
PIT HARDENING
February
March
April
May
June
July
August
September
October
November
FLOWER INDUCTION
MAXIMUM RATE OF PIT HARDENING (6-10 WAB)
HARVESTING

Figure 9

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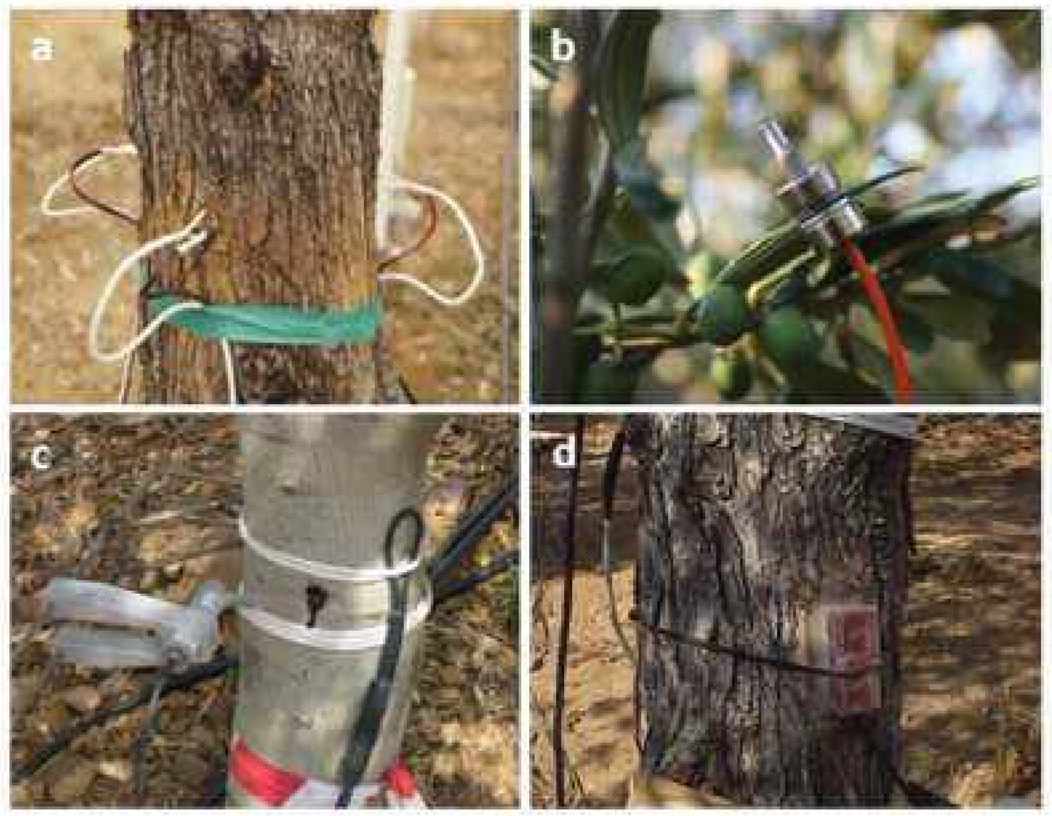

Table 1

Table 1 Water productivity values, in terms of fresh fruit and oil, reported for different olive cultivars and growing conditions. FI = full irrigation; SDI= sustained deficit irrigation; RDI = regulated deficit irrigation. The number before SDI and RDI indicates the aimed water supply, expressed as percentage of that for the FI treatment (the actual amounts varied slightly).

	Crop characteristics			**Water productivity ($kg\ ha^{-1}\ mm^{-1}$)**	
Reference	**Cultivar & *location***	**Water regime**	**Plant density (trees ha^{-1})**	**Fresh fruits**	**Oil**
Moriana et al. (2003)[1]	Picual	FI	278	22.0	5.0
	South Spain	Rainfed		9.0	0.2
Tognetti et al. (2007)[2]	Frantoio	FI	555	56.0	13.3
	Central Italy	60RDI		68.0	16.0
Iniesta et al. (2009)[3]	Arbequina	FI	408	33.0	4.5
	South Spain	25SDI		80.7	13.2
		25RDI		94.2	14.6
Correa-Tedesco et al. (2010)[4]	Manzanilla	FI	312	18.0	
	Northwest Argentina	60SDI		21.0	
Ramos and Santos (2010)[3]	Cordovil	FI	69	2.6	0.5
	South Portugal	50SDI		6.8	1.4
Fernández et al. (2013)[5]	Arbequina	FI	1666	40.6	2.5
	South Spain	60RDI		51.4	2.8
		30RDI		86.3	6.4

[1] Average of ‘on’ and ‘off’ years with no alternate bearing.

[2] Sub-humid area with an average yearly rainfall of 722 mm.

[3] Average of ‘on’ and ‘off’ years with marked alternate bearing.

[4] 7-year-old, not fully productive trees.

[5] Average of 3 years, no alternate bearing.

Table 2

Table 2 Relationships between fruit and oil yields and water consumed by the crop, for different olive cultivars and growing conditions. ET_c = crop evapotranspiration IA = irrigation amount. E_p = plant transpiration. $R^2 = r^2$ = coefficient of determination.

Reference	Orchard type	Relationship between yield and water consumed
Moriana et al. (2003)	Mature 'Picual' 278 trees ha^{-1} South Spain	Fruit yield $= -16.84 + 0.063\ ET_c - 0.035 \times 10^{-3}\ ET_c^2$ $R^2 = 0.71$ Oil yield $= -2.78 + 0.011\ ET_c - 0.006 \times 10^{-3}\ ET_c^2$ $R^2 = 0.59$ (Yield in t ha^{-1}; ET_c in mm $year^{-1}$)
Grattan et al. (2006)	Young[1] 'Arbequina' 1709 trees ha^{-1} California	Fruit yield $= 128.72 + 23.147\ IA - 0.0215\ IA^2$ $R^2 = 0.79$ Oil yield $= -\ 98.243 + 2.5481\ IA - 0.00215\ IA^2$ $R^2 = 0.94$ (Yield in kg ha^{-1}; IA in mm)
Martín-Vertedor et al. (2011a)	Young[2] 'Morisca' 417 trees ha^{-1} Southwest Spain	Fruit yield $= 0.078E_p - 2.524$ $r^2 = 0.63$ (Yield in kg $tree^{-1}$; E_p in mm $year^{-1}$)

[1] Relationships apply to the 2nd harvest (trees not fully productive yet).

[2] The relationship applies to 4 to 6 year old trees (not fully productive yet).