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

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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.

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 1980s, in the number of research groups focussed on understanding the biology of this species and its response to the environment, as well as on 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), and 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

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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_{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
ET_c	crop evapotranspiration
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
$g_{s\text{-max}}$	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
RWC_{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
$V_{c\text{-max}}$	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

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 to −8 °C can cause damage to olive, although resistance to temperatures as low as −18 °C 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 °C, 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 °C, 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).

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