

Response of olive trees to drought

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Summary

Olive trees are able to take up, transport and transpire water at soil moisture contents which are usually too low to maintain these processes active in other fruit tree species. There are several mechanisms that allow the olive tree to withstand long periods of drought, high temperatures and high irradiance regimes. In this paper the main aspects of the water relations of the olive tree are reviewed, and in particular water transport in the xylem conduits, stomatal regulation and osmotic adjustment.

Introduction

Olive (*Olea europaea* L.) is a typical evergreen sclerophyllous species of the Mediterranean basin, well adapted to areas with a long, hot growing season and a relatively cool winter, but where limited or none support of water for irrigation is generally available. Olives are, in fact, considered drought tolerant. Some anatomical characteristics such as stomatal location in depressions of the leaves, the small dimensions of the leaves and their thickness and leathery consistence together with waxy cuticle and the presence of hairs on the leaf surface, certainly contribute to this drought tolerance habit. Nevertheless, an ecophysiological approach can reveal some aspects of olive adaptation to drought that are worthwhile to be studied in depth. According to relevant new studies on these aspects it seems that this species faces seasonal and diurnal water stress by adopting a drought resistance strategy based upon tolerance, with strong efforts in terms of metabolic investments in the root system at expenses of vegetative and reproductive performances. On the basis of some of these findings the general view of olive as a species "well adapted to drought" should be carefully reconsidered. Indeed, it appears to be very *sensitive* to water stress but even very *tolerant* to the effects of this stress.

In this paper the main aspects of the water relations of the olive tree are reviewed, and in particular water transport in the xylem conduits, stomatal regulation and osmotic adjustment.

Relation between xylem structure and functionality

The functionality of xylem pathway relies on the xylem structural characteristics. Olive wood is classified as diffuse-porous, in fact vessels are distributed quite uniformly in the annual growth rings. In olive wood the amount of fibers is considerably high while the amount of parenchyma is low. The diameter of xylem vessels is generally small (<40 µm), and almost 90% of the vessels has a diameter less than 20 µm in the node and internode portions of one-year shoots (Lo Gullo e Salleo, 1990). More than 90% of the xylematic elements has a length less than 22 µm, but the distribution of frequencies shows high values of length along the entire range between 0 and 22 µm. Hence, the single elements are narrow and relatively long,

compared to other Mediterranean tree species (*Ceratonia siliqua*, *Laurus nobilis*, *Quercus ilex*, *Quercus pubescens*, *Quercus suber*) (Lo Gullo e Salleo, 1990).

The small diameter of xylem vessels is a strategic morphological trait to withstand drysoil conditions. This character allows olive trees to reduce the probability of emboli production in the conducting system. In fact, as a consequence of soil water depletion and of the reduction of water potential a partial tissue dehydration and an interruption of the continuity of the water columns within the xylem vessels can occur following the formation of microbubbles. They rapidly expand (cavitation) occupying the vessel lumen and determining vessel embolism and consequently the loss of functionality. If the number of the vessels that undergo this phenomenon is high then xylem water transport is severely affected and the soil-plant-atmosphere *continuum* is interrupted.

In olive, at values of water potential corresponding about at cell turgor loss point about 5% of the stem xylem vessels loses its functionality because of the emboli presence. Consequently, since the vessels with a larger diameter are the first that undergo to cavitation (Salleo e Nardini, 1999), stem hydraulic conductivity is reduced by 25-30%. The less susceptibility of the olive hydraulic system to cavitation during drought periods is coupled with a low efficiency in water and nutrient transport via the xylem because the flow is function of fourth power of the radius of the single vascular element.

In olive trees, the low conductivity determines high hydraulic resistances in the stem and in the root compared to those of other tree species.

Under water shortage not only the root-to-shoot (R/S) ratio is increased but also root anatomical characteristics are modified together with the water flow through the root. In trees grown under wet and dry water regimes complete transition to secondary growth was found closer to the apex in the roots grown in dry soil than in the roots grown under irrigation. Furthermore, in dry soil the root cortical cylinder was wider than in watered soil, although it is still unclear whether this last aspect may be related to water shortage or to mechanical stress exerted by the dry soil (Fernandez et al., 1994).

Soil water availability determines olive root distribution and activity. In fact, under dryland conditions the water uptake is prevailing from the deepest portion of root system whereas under irrigation or after irrigation of trees previously in rainfed conditions the greatest amount of water is taken up by the surface root system. Moreover, in irrigated trees the highest values of water flow are measured in the outer part of the root conducting cylinder, whereas in non-irrigated trees in the inner part (Fernandez e Moreno, 1999).

Leaf water potential variation

Olive leaf water potential (Ψ_w) has considerably high variation both on daily and seasonal basis. During the day stomata can only partially regulate transpiration, thus daily Ψ_w variation reflects both tissue water status and environmental evapotranspiration demand. The pronounced diurnal reduction of Ψ_w is due to the loss of water by the tissues, to the high stem hydraulic resistances and to the hardness of leaf cell walls. As a result Ψ_w reaches values close to the point of turgor loss in the hottest hours of the day even in good moist condition of the soil.

The leaf cell turgor loss point has been estimated of about $-3.0-3.5$ MPa of Ψ_w corresponding to 75-80% of relative leaf water content. Water potentials of about $-8-10$ MPa have been measured in extreme water deficit conditions and surprisingly even at such kind of values trees are still able to recover their water status (Angelopoulos et al., 1996).

Leaf water potential and tissue water content in the tree undergo cyclic variation on a daily basis. During the morning water uptake by the root system is less than the canopy transpiration, thus a progressive tissue dehydration occurs. As a consequence of a water shortage it has been estimated that olive leaves can lose until the 60% of their water content with transpiration (Xiloyannis et al., 1998). During the afternoon and

the night olive tree the amount of water taken up is higher than the amount of water transpired with a consequent rehydration of its own tissues. The hysteresis behaviour of the relation between water consumption and tissue water content indicates that water stored in the tree during night-time is utilised during day-time to partially support transpiration and photosynthetic activity of the canopy. The remarkable daily variation of stem diameter can be measured with suitable sensors and be used as a basis for the irrigation management of the olive orchard.

Stomatal regulation

Stomatal density in olive is between 200 and 700 mm⁻² depending upon the variety. In olive leaves stomata are located only in the abaxial surface of the fully expanded leaf. Stomatal conductance (g_s), an indicator of leaf permeability to leaf-atmosphere gas exchange, in good water soil conditions shows average values when compared to other tree species. Thus, olive leaf transpiration rate is not particularly low when water is not a limiting factor. As soil water declines olive g_s is maintained at quite high levels, higher than those of other species like apricot and kiwi that have stomata particularly sensitive both to the decrease of Ψ_w (Fig. 1) and to the increase of vapour pressure deficit between the leaf and the atmosphere (VPD). It's worthwhile noting the wide range of Ψ_w values that olive tree is able to tolerate, whereas small Ψ_w variations can be tolerated by apricot and kiwi trees. Furthermore, the slope of the g_s/Ψ_w curve in olive is lower than the other two species indicating that olive stomata remain partially open even when the tree is experiencing severe water stress conditions (Fig. 1). This behaviour allows the tree to maintain a certain photosynthetic activity together with a certain degree of canopy thermoregulation.

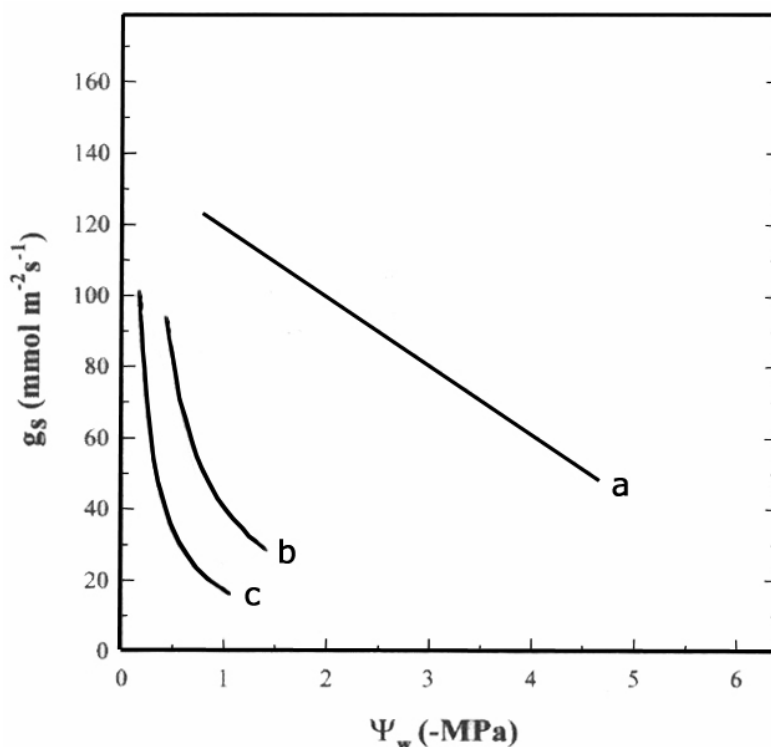


Figure 1 – Relation between pre-dawn stomatal conductance (g_s) and leaf water potential (Ψ_w) in potted kiwi (C), apricot (B) and olive trees (A).

The reduced soil water availability modifies the g_s diurnal pattern. If olive trees are well watered and VPD is not particularly high, g_s pattern is described by a bell-shaped asymmetric curve, with the maximum stomatal aperture at about the end of the morning period (Fig. 2). On the contrary, if the trees are severely stressed, g_s shows very low values along the entire diurnal period and the maximum is reached within two hours after sunrise. In such a condition is possible sometimes to observe a slight stomatal re-opening late in the afternoon. This behaviour tending to a bimodal curve is fully expressed if water stress degree is low (Fig. 2) or, in well watered olive trees, if VPD and temperature reach very high values in the midday, as it normally occurs in the Mediterranean climates. The reduction of stomatal degree of aperture during midday is more or less relevant depending upon the water deficit level reached by the tree and upon climatic conditions.

Osmotic adjustment

Osmotic adjustment (or osmoregulation) is the ability of the cell to synthesise and to accumulate solutes osmotically active and metabolically compatible that allow the plant to reduce the osmotic potential in a way to eventually reduce the effects of environmental stresses. In other words cell turgor is maintained by means of increases in cell solute concentration. As the soil water content decreases olive tree shows a high degree of osmotic adjustment (up to 1.5 MPa), which allows the tree to reduce the effects onto cell turgor caused by Ψ_w reduction. Osmotic adjustment in olive trees subjected to water deficit is mainly due to mannitol, glucose and organic acid accumulation in the leaves (Gucci et al., 1998).

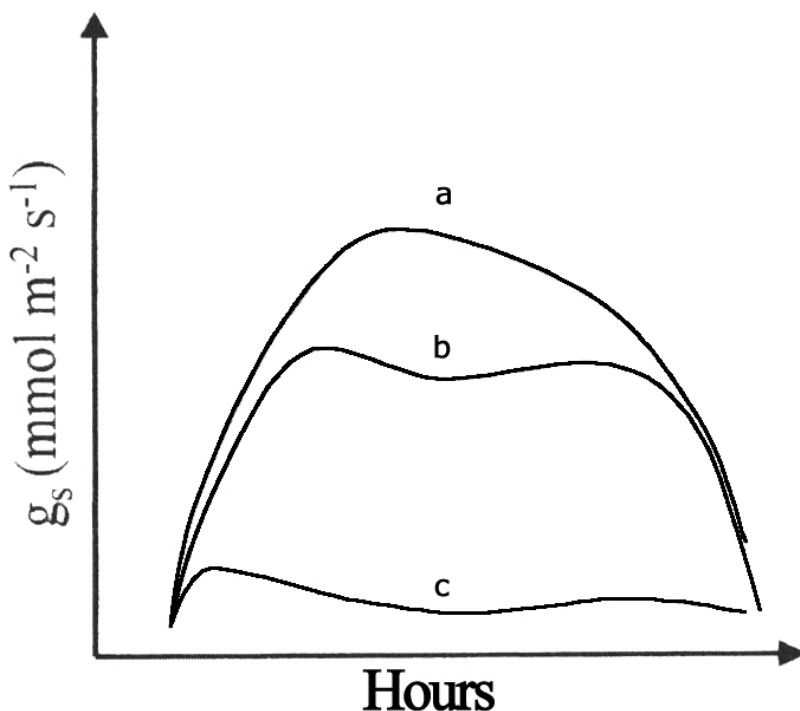


Figure 2 - Typical diurnal patterns of stomatal conductance (g_s) in potted olive trees. Curve A indicates plants irrigated with an amount of water equal to the daily average evapotranspiration, curve B plants irrigated with 50% of the daily average evapotranspiration, and curve C plants not irrigated for ten days.

Both osmotic adjustment and Ψ_w reduction, also due to the lack of elasticity of olive leaf cell walls, increase potential gradient between the canopy and the root system, making possible water uptake from the soil at very low levels of soil water potential.

Conclusions

The results from up to date research activities onto olive tree biology have made possible to clarify some of the main mechanisms involved in olive tolerance to long periods of drought and in its ability to utilise water efficiently. A complex of phenomena such as the small diameter of the vessel elements, the high capacitance of the tissues, the slow stomatal response, the low vessel cavitation probability, the low osmotic potential and the low leaf water potential make altogether this a particular species both under the agronomic and biological point of view. The anatomical and structural characteristics of the hydraulic system of this species represent an optimal compromise between the needs of efficient water transport and the need for reducing vessel cavitation probabilities.

There is increasing evidence that such kind of ecophysiological approach can be effective for fully understanding how to manage olive orchard in the near future, specially in the Mediterranean environments where drought constitutes a serious limiting factor affecting olive productivity.

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