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Letter to the Editor

More than Stomata: Trichomes, Xylem, and the Architecture of Water Use in Olive

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Stomatal regulation refers to the process by which Olive (*Olea europaea*) plants acquire the ability to resist drought. During periods of water depletion, carbon acquisition, transpiration, and photosynthesis are affected, since water availability status has a profound influence on stomatal conductance [1]. In general, field observations have shown that a decline in plant water status leads to a decrease in stomatal conductance. However, it is insufficient to interpret olive water use as a stomatal phenomenon alone, because anatomical and hydraulic structures enable water to reach and interact with the leaves [2].

While stomatal closure is an adaptive mechanism through which several plant species cope with drought conditions, in olive, it is insufficient, as the leaves of olive possess specialized epidermal surfaces, as well as trichomes. Furthermore, water transport to the stem and leaves in this plant occurs via an interconnected xylem network, highlighting that the complexity of the hydraulic network extends beyond xylem tissues. Therefore, to envisage water use in olive plants, an integrated system encompassing stomatal regulation, leaf anatomy, trichome architecture, and hydraulic function would adequately explain the physiological and developmental changes that olive leaves undergo during drought [3].

According to Bacelar *et al.* [4], the stomatal responses of olive leaves during drought, i.e., the change of stomata size and density under water limitations, indicate the presence of stomatal response developmental plasticity, as well as a rapid regulation of gaseous exchange. Additionally, field-grown olive cultivars differ from each other regarding their anatomical traits, stomatal attributes, cuticular development, and sclerophylly [4]. This observation is important since it shows the difference between short-term stomatal control and long-term anatomical adjustments in regulating drought resistance in olive. A significant deduction from cultivar-specific responses to water limitations is that there is no specific universal leaf phenotype that can explain drought resistance in olive plants. It is therefore preferable to deduce that drought resistance emerges from olive plant modifications that balance water conservation and carbon gain.

The architecture of water use in olive plants ought to include trichomes, as this component remains ignored in discussions. Bosabalidis & Kofidis [3] and Ennajeh *et al.* [5] stated that olive leaves have dense peltate trichomes that are non-glandular. These trichomes are found densely on leaves during water limitation [3, 5], however, environmental factors, such as wind, affect trichomes in playing a direct role in transpiration reduction, even though they alter boundary layer properties in olive [6, 7]. Furthermore, since the trichomes on the abaxial leaf surface exhibit structural and chemical heterogeneity, the likelihood of them directly interacting with externally supplied water is greater [8]. This intensifies the likelihood of foliar water absorption by trichomes in olive plants as well [9], indicating that olive plants use trichomes to adapt to drought conditions by either modifying the fate and availability of water deposited on the leaf surface, or by decreasing the rate of water loss by

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evaporation. Therefore, the hydraulic pathway used by olive plants is complex and undergoes various changes during drought in order to conserve water and protect the distal organs of the plant [2]. During hydraulic segmentation, hydraulic conductance, hydraulic signalling, and xylem function become altered [10]. Although the relationship between these 3 factors is straightforward, the relationship between hydraulic changes and stomatal closure isn't as straightforward [2]. However, it's a fact that the stems retain greater functionality than the roots and leaves when they are subjected to stress conditions during hydraulic segmentation [11].

Among wild olive genotypes, hydraulic traits are linked to photosynthetic performance and growth patterns [12], however, embolisms found in the xylem due to extreme drought arise as a safety mechanism formed through osmotic adjustment and vulnerability to hydraulic dysfunction in the xylem [13]. This shows that xylem safety is not a determinant of drought resistance in olive. Hence, there is a need to consider the entire hydraulic pathway. Li *et al.* [14] state that embolism vulnerability between the leaves and petiole in *O. europaea*, and other angiosperms was very similar, highlighting the need to assess the interaction between the xylem, extra-xylary tissues, veins, stomata, and leaf-surface properties to protect the distal tissues from dehydration [15]. Additionally, there is a possibility that there is an interconnectedness between leaf and branch hydraulic architecture, instead of an individual anatomical trait being altered during drought conditions.

Olive leaves are sclerophyllous, and while they contain all the characteristics of an ordinary leaf, their traits are modified during water limitations [4, 5]. Some of the modifications that occur are changes in epidermal thickness, palisade and mesophyll structure, leaf area, tissue density, as well as cuticular characteristics [12]. These changes are found to make photosynthesis in the mesophyll tissues under stress unsustainable. Furthermore, this difficulty is associated with water conservation and carbon dioxide diffusion problems caused by modification of the epidermal thickness. However, each cultivar responds differently to water stress, e.g., 'Chemlali' and 'Meski' cultivars [16]. Therefore, it's unwise to define drought resistance through a single trait, such as stomatal conductance, because variations in physiological, anatomical, and water-use response are possible between different Olive cultivars [12].

I decided to write this letter because hydraulic traits, stomatal behaviour, and anatomical allocation (e.g., leaf anatomy, trichome characteristics) in olive plants ought to be considered as part of a larger functional system in response to water stress. By taking this into account, olive breeding and water management strategies will become more organized, and perhaps be performed with greater confidence. In my opinion, drought tolerance in olive is an architectural property, as water moves through a continuum from the roots and xylem to the veins, mesophyll, epidermis, and trichomes. In addition to the above, experiments involving controlled humidity and wetting regimes will result in answering questions pertaining to water conservation strategies in olive, particularly those directed toward the olive water economy. These experiments will assist in understanding the general principles of how carbon gains and hydraulic rate are balanced in long-lived woody plants. As a final remark, it should be understood that the leaf surface is not merely a stomatal surface; rather, it's an anatomical and hydraulic interface where the stomata, trichomes, and xylem converge.

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