



Assessing environmental controls over conductances through the soil–plant–atmosphere continuum in an experimental olive tree plantation of southern Italy

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ABSTRACT

Constraints on plant water status and water use indicators were studied in orchard grown *Olea europaea* L. trees, cv. Nocellara del Belice, in order to assess productivity and drought adaptation. The study was conducted on 16-year-old grafted plants, grown under different water treatments for 14 years in an experimental site plantation in southern Italy. Water treatments were: a non-irrigated, rainfed, control (T0) and three treatments that received seasonal water amount equivalent to 33 and 66% of crop evapotranspiration (ET_c) from the beginning of pit hardening to early fruit veraison (respectively T33 and T66), and 100% of ET_c throughout the irrigation season (T100). During 2006 and 2007 growing seasons, plants were continuously monitored by automatic point dendrometers measuring stem radius variation and whole-plant water use was determined using a xylem sap flow method (compensation heat-pulse technique). Additional ecophysiological parameters, such as stomatal conductance and water potentials were periodically measured, as well as vegetative development. Predawn leaf water potential decreased in rainfed trees and this was associated with increasing soil moisture deficit, while the difference between predawn and midday leaf water potentials increased, suggesting anisohydric regulation of plant water potential. Olive trees exhibited a tight stomatal control over transpiration, but insufficient to prevent loss of hydraulic conductance under severe drought stress. The stem radial increment and sap flux did not differ consistently between water treatments in the mild year (2006), while irrigated trees had higher water use than rainfed trees in the dry year (2007). However, plants growing under rainfed conditions showed a small increase in maximum daily shrinkage during drought periods compared to irrigated ones, although no marked differences were recorded between irrigated treatments. The mean daily transpiration rate, canopy conductance and decoupling coefficient were higher in 2006 than in 2007, the driest year, only, and in fully irrigated rather than rainfed plants. These results support the idea that rainfed trees had more conservative water use strategies than irrigated trees, and that deficit-irrigated trees acclimated somewhat functionally and structurally to long-term partial watering. Based on these observations, we can argue that loss of hydraulic conductance is an important mechanism for increasing stomatal control of transpiration under progressive soil drying. Another view implies that the increasing difference between soil and leaf water potential during summer induced stomatal closure and minimized the risk of a collapse of the conductive system, decreasing transpiration and reducing hydraulic conductance.

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1. Introduction

The olive tree (*Olea europaea* L.) is notable for its drought resistance, though its degree of control over water loss under stressful conditions depends on structural and functional proper-

ties that have been rarely quantified in field studies resembling commercial plantations subjected to long-term management practices (Fernández et al., 1997; Moriana et al., 2002; Tognetti et al., 2005). In olive trees growing in Mediterranean-type agroecosystems characterized by a marked lack of predictability of rainfall, features related to regulation of water utilization and water balance are key components of adaptation to the environment and knowledge of these features is required to establish reliable irrigation-scheduling protocols (Naor, 2006; Fernández

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et al., 2008). Within Mediterranean countries, as in other parts of the world, the expansion in the area of modern olive tree plantations has generated concerns about risks associated with unsustainable irrigation practices, as well as the potential environmental consequences, in particular the effect of plantations on local water balance.

The greatest xylem tension experienced by a tree during the course of the year is defined as its minimum seasonal water potential, which is a plant physiological property that emerges from the balance between soil water availability, foliage transpiration rate, and xylem transport efficiency (Bhaskar and Ackerly, 2006). However, the minimum water potential also acts as a selective force on xylem structure that, in turn, generates functional associations with a number of hydraulic traits. Transpiration and leaf water status are coordinated with tree architectural features to minimize plant water loss and avoid hydraulic failure (Sperry et al., 2002). Differences in stomatal conductance at the leaf level and transpiration at the stand level suggest that water use and whole-tree conductance might change with management practices applied to olive groves (Tognetti et al., 2004, 2005). Such differences might be caused by changes in the hydraulic conductance of the soil-to-leaf pathway because of the differences in path length and in sapwood permeability (Orgaz et al., 2007). Yet, changes in the relationship between potential evaporative demand (leaf area) and water replenishment capacity (root biomass) could influence the sensitivity of stomata to vapour pressure deficit (Thomas et al., 2000). Thus, reductions in leaf area through pruning and training within olive tree plantations have the potential to regulate stomatal behaviour as plant water status declines, reducing the rate at which water stress develops at a given vapour pressure deficit.

Plant water deficit closes stomata and thus reduces net CO₂ assimilation, but it also inhibits cell division and cell expansion (Hsiao, 1973; Abe et al., 2003). These two sides (carbon and water) are closely interrelated and have the potential to limit growth and yield of plants, either individually or in combination (Giovannelli et al., 2007). Limitations may be driven directly by low tissue water potentials (Boyer, 1985; Proseus and Boyer, 2005) or indirectly by signals transported from roots under drought (Davies and Zhang, 1991). To maintain the physiological activity, plants must be able to supply water from the soil to leaves to balance losses by transpiration or, alternatively, withstand extreme tensions generated in the xylem due to water loss, integrating the effects of both soil water availability and atmospheric evaporative demand. So far, owing to the coupling between water relations and climatic conditions, the response of plant water status to several fluctuating environmental variables is dynamic (Hinckley and Bruckerhoff, 1975). Transpiration is often proportional to tree growth and leaf area index, thus controlling maximum productivity, but the long-term acclimation of the hydraulic system to resource availability is uncertain, being affected by the balance between leaf area and sapwood area (Samuelson et al., 2007). For example, Mencuccini (2003) proposed that whole-plant hydraulic efficiency might decrease with increasing resource availability. In theory, high whole-tree hydraulic conductance per unit leaf area would maintain leaf water status as water potential declined. Inferences drawn from leaf level measurements concerning physiological adaptations at the whole-plant level can be confounded by interactions among unrecognized variables operating at other scales (Meinzer, 2003). In the long term, the control over leaf water status, minimizing variations as soil dries or as evaporative demand increases, may be achieved through changes in leaf area and root extension, and in the shorter term through changes in leaf angle, stomatal conductance, and hydraulic properties of the transport system (Jones, 1990).

Use of sap flow methods allows determining transpiration from individual trees. By monitoring sap flow in a number of trees, it is possible to use either sapwood area, diameter at breast height or leaf

area index of a site to up-scale from tree-scale estimates of water use to stand-scale estimates of water use (Wullschlegel et al., 1998). Continuous recording of sap flow rate (Nadezhdina et al., 2007) and trunk shrinkage variation (Moreno et al., 2006) in olive plantations might provide indirect measurements of plant water status, and represent a promising integrated tool for the development of automated monitoring systems that determine irrigation needs in real time or at least at frequent intervals in olive trees (Moriana and Fereres, 2002). Moderate levels of water stress applied to olive trees, by withholding irrigation during the period of slow fruit growth, have been shown to preserve fruit and oil yields, while controlling excessive vegetative vigor, without detrimental effects on crop quality (Tognetti et al., 2006, 2007). Water shortage imposes improvements of water use efficiency that implies a requirement for increased precision in irrigation control, maintaining the soil moisture status within fine bands to achieve specific objectives in crop management (Jones, 2004), particularly when using irrigation also for control of vegetative growth, as in deficit irrigation.

In the current study, we examined patterns of water potentials and stomatal conductance, soil water deficits and vapour pressure regime, trunk shrinkage and plant transpiration in mature (>10 years old) rainfed and irrigated olive trees growing at the same site and under similar atmospheric conditions. The aim was to better understand the relative importance of atmospheric and hydraulic controls on plant water use. In particular, we tested the hypothesis that long-term hydraulic acclimation of olive trees to deficit irrigation is defined by the temporal variation in regularly recorded tree-based water status and water use indicators, such as stem radial variation and xylem sap flow. Elucidation of specific factors driving water consumption and trunk shrinkage of individual olive trees is probably hampered by covariance and interaction among environmental drivers. Specific objectives of this research were to (i) quantify the seasonal patterns of conductances; (ii) determine the processes controlling conductances; (iii) assemble these processes in a framework suitable for application in modelling schemes.

2. Materials and methods

2.1. Study site and experimental design

The experiment was conducted in the summers of 2006 and 2007 on mature olive trees (*O. europaea* L.) of the cv. Nocellara del Belice (used either for oil or picking) at the experimental farm of CNR-ISAFOM, located near Benevento (41°06', 14°43' E; 250 m a.s.l.), a typical olive growing area of southern Italy. The site is flat and the trees are planted in rows 6 m apart, at a tree spacing of 3 m. The plantation was established in 1992 with 1-year-old plants, grafted on DA 12 I° clonal rootstock (patent CNR no. 1164/NV). Trees are clean cultivated and trained using the central leader system (Fontanazza, 1994), and they have been pruned every year according to standard procedures for this training system. The climate is Mediterranean (Table 1), with a mean annual rainfall of 729 mm, which was an average of 43 rainy days for which rainfall was larger than 5 mm within a 24 h period (23-year average, 1985–2007); the amount of precipitation is rather stable (714 and 754 mm, respectively for the last 10- and 5-year average). Overall, the daily mean temperature rises from 10.8 °C in April, to 22.5 °C in July, and decreases to 14.4 °C in October. The yearly mean reference evaporation is on average 1232 mm (23-year average, 1985–2007). The soil is sandy loam (organic matter 1.76%, CaCO₃ 1%, N 0.15% and pH 7.2), characterized by volumetric water content of 0.356 m³ m⁻³ at field capacity (soil matric potential of -0.03 MPa) and 0.212 m³ m⁻³ at wilting point (soil matric potential of -1.5 MPa), whereas the bulk density is 1.25 Mg m⁻³. In the beginning of the season, soil water content at field capacity was measured soon after irrigation (nearby emitters).

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