



Effects of reduced irradiance on hydraulic architecture and water relations of two olive clones with different growth potentials

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ABSTRACT

The hydraulic architecture and water relations of two olive genotypes, 'Leccino Dwarf' (LD) and 'Leccino Minerva' (LM) growing at two irradiance levels i.e. full sunlight irradiance (HI) and 50% sunlight irradiance (LI) were studied. The two clones showed similar plant hydraulic conductances (K_{plant}) and similar conductance of roots and leaves (K_{root} and K_{leaf}) when growing at equal irradiance levels. However, both K_{plant} and K_{root} were significantly lower in LI plants than in HI ones. On the contrary, K_{leaf} was unaffected by the light regime. One-year-old twigs of LI plants produced longer xylem conduits but lower average diameter of conduits and less conduits per unit xylem cross-sectional area compared to HI plants. As a consequence total conductive cross-sectional area of twigs was computed to be about 16% smaller in LI individuals than in HI ones.

The LM genotype resulted potentially more vulnerable to cavitation than the LD one, although shading did not influence this variable. Shading influenced root biomass negatively with stronger reduction in LM genotype than in LD one. Although transpiration rates were substantially lower in shaded than in HI plants minimum diurnal leaf water potential was about -1.2 MPa for both clones regardless the irradiance regime. Our conclusion is that the hydraulic efficiency of both olive clones was adjusted to meet the evaporative demand imposed by the irradiance regime with consequently similar equal hydraulic sufficiency.

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1. Introduction

In modern orchard management, grafting techniques are widespread. The rootstock is usually selected for performance in different soil types whereas the scion is selected in the view of obtaining high productivity and/or quality of fruits (Cohen and Naor, 2002). Low-vigour rootstocks are increasingly used in high-density orchards with the purpose of reducing the scion growth potential with consequent reduction of cultural costs associated with harvesting and pruning (Troncoso et al., 1990; Webster, 1995; Tous et al., 1999). Recent studies suggest that the dwarfing effect on the scion as induced by low-vigour rootstocks is related to constraint on the 'hydraulic architecture' of grafted plants (e.g. Atkinson et al., 2003; Basile et al., 2003; Clearwater et al., 2004; Nardini et al., 2006; Cohen et al., 2007). The term 'hydraulic architecture' first coined by Zimmermann (1978) refers to the partitioning of hydraulic conductances in a plant and includes changes in xylem efficiency and vulnerability to cavitation (Tyree and Ewers, 1991).

It is generally agreed that hydraulic architecture influences plant water relations and growth potential (e.g. Hubbard et al., 1999; Sperry, 2000; Meinzer, 2002) in that plants with high hydraulic conductance undergo smaller water potential drops between leaves and roots and run lower risk of xylem cavitation which favours gas exchange and growth (Tyree, 2003). In turn, plant hydraulic properties vary in response to several environmental factors including water and nutrient availability (Cruziat et al., 2002; Ewers et al., 2000) and irradiance (Cochard et al., 1999; Barigah et al., 2006). Any of these factors may profoundly affect the hydraulic efficiency of plant organs. As an example, water stress has negative effects on radial water transport in the root (Lo Gullo et al., 1998), triggers xylem cavitation (Sperry and Tyree, 1988; Sperry and Ikeda, 1997) and may cause vein collapse and aquaporin inactivation in the leaves (Cochard et al., 2004; Kim and Steudle, 2007). Plasticity in the response to environmental factors involves morpho-anatomical changes e.g. in xylem conduit dimensions and root-to-shoot ratio and is age-dependent (Barigah et al., 2006). Variations of plant hydraulic efficiency have also been measured over the short term as a consequence of cycles of xylem embolism and refilling (Salleo et al., 2004), modifications of xylem sap ionic concentration (Zwieniecki et al., 2004) or as the result of

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expression/regulation of aquaporins (Henzler et al., 1999). Recent studies have shown that light regulates the hydraulic properties of roots and leaves both over the long (Tyree et al., 1998; Sack et al., 2005) and the short term (Lo Gullo et al., 2005; Cochard et al., 2007).

Several studies have been conducted on crops grafted on low- and high-vigour rootstocks with contrasting results in terms of effects of changes in plant hydraulics as determined by the rootstock's vigour. In some species (e.g. *Malus domestica* L., Atkinson et al., 2003), dwarfing included decrease in whole-plant hydraulic conductance (K_{plant}) which may depend on decrease in root hydraulic conductance (Nardini et al., 2006). By contrast, Clearwater et al. (2004) have shown that the scion growth potential of *Actinidia* was independent on plant hydraulics. In the case of *Olea europaea* L., the genotype 'Minerva' of the cultivar Leccino (LM) known for good oil quality, high and constant productivity, resistance to pathogens and tolerance to a wide range of habitats (Marsilio and Lanza, 1988; Del Río et al., 2000, 2003) has been measured for hydraulic architecture when grafted on 'Leccino Dwarf' (LD) which is a genotype characterized by strongly reduced vegetative growth. This scion/rootstock combination showed low hydraulic conductance of the rootstock which effectively depressed the scion growth (Nardini et al., 2006). Nonetheless, although the dwarfing effect reduced the transpiring surface of the grafted plant, no clearly increased resistance to xylem cavitation of the scion was observed in LM/LD combinations (Trifilò et al., 2007).

In the Mediterranean Basin area where olive cultivation is widespread, plant growth is not only limited by summer water scarcity but also by high irradiance causing chlorophyll degradation and reduction in photosynthesis, in particular during the juvenile period (e.g. Gussakovsky et al., 1993; Jifon and Syvertsen, 2001, 2003; Blanke, 2002). For this reason, it is a common cultivation practice to protect young individuals in the nursery using shading nets until plants are transferred to the field. Shading has been reported to induce increase of productivity, gas exchange and photosynthetic rate, as well as resource allocation (e.g. Sasaki and Mori, 1981; Popma and Bongers, 1988; Bjorkman and Demmig-Adams, 1994; Cohen et al., 1997, 2003, 2005; Stanhill and Cohen, 2001; Medina et al., 2002; Raveh et al., 2003). By contrast Barigah et al. (2006) have found that saplings of six forest trees grown under severe shading (4–36% of full sunlight) showed increased vulnerability to xylem cavitation, decreased K_{root} and K_{plant} as well as the root-to-shoot ratio with quantitatively different species-specific responses to reduced irradiance. Accordingly, Nardini et al. (2005) have shown that woody and herbaceous species adapted to shade conditions showed lower leaf hydraulic conductance than sun-growing species due to narrower vein conduits in the former. This feature was interpreted as a consequence of low water demand in shade-growing plants.

Previous studies by some of us (Nardini et al., 2006; Gascò et al., 2007; Lovisolò et al., 2007; Trifilò et al., 2007) on olive genotypes with different growth potentials (see below) and on their grafting combinations have revealed the need of a better understanding of changes in hydraulic architecture as influenced by environmental factors in the view of correctly interpreting the influence of the rootstock vigour on scion growth potential. On the basis of the above studies, saplings of the olive genotype 'Leccino Dwarf' (LD) and the vigorous 'Leccino Minerva' (LM) were compared for hydraulic architecture when under the effect of shade conditions commonly used in olive nurseries (50% of full sunlight, see below). In particular, the hydraulic conductance of whole plants (K_{plant}) was measured as partitioned between roots (K_{root}) and leaves (K_{leaf}) that are thought to be the sites of major hydraulic bottlenecks in a plant (Nardini and Tyree, 1999). Shading conditions were also studied as potentially modifying xylem conduit dimensions and vulnerability to cavitation, leaf water status, gas exchange and growth.

2. Material and methods

2.1. Plant material and growing conditions

All experiments were conducted in July 2007 on two genotypes of *Olea europaea* cv Leccino characterized by different growth potentials (see above) i.e. Leccino 'Minerva' and Leccino 'Dwarf' (LM and LD, respectively, Nardini et al., 2006; Gascò et al., 2007). One year before experiments (July 2006), 20 plants per genotype two years of age were transferred to an experimental field in Sciacca (Sicily, southern Italy) in 3000-L containers filled with a 3:2 (v/v) mixture of peat and fine pumice stone. Plants of each genotype were divided into two groups one of which was grown in full sunlight (high irradiance, HI) while the second one was grown at 50% solar irradiance (low irradiance, LI). Reduced irradiance was obtained by covering plants with shading nets and was estimated by measuring the photosynthetically active radiation (PAR) with a quantum sensor (LI190S1, LiCor Inc., Lincoln, NE, USA) at 10 cm from the top of the canopy. Shading nets effectively reduced maximum daily irradiance from about $1900 \mu\text{mol m}^{-2} \text{s}^{-1}$ (full sunlight) to $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ (shade). The soil was fertilized with 2 kg m^{-3} of a commercial slow-release N, P, K fertilizer and 2 kg m^{-3} of Biotron (Cifo S.p.a., S. Giorgio di Piano, Bologna, Italy). All plants were kept well irrigated throughout the study period by irrigating soil to field capacity twice per week.

2.2. Gas exchange and plant water status

Maximum transpiration rate (E_L) and minimum diurnal leaf water potential (Ψ_{min}) were measured between 12.00 and 14.00 h of two successive sunny days on ten leaves from different plants of each genotype under study at each irradiance level tested using a steady-state porometer (LI-1600, LiCor Inc., Lincoln, NE, USA) and a portable pressure chamber (3005 Plant Water Status Console, Soilmoisture Equipment Corp., Goleta, CA, USA), respectively. Air temperature (T_{air}) and relative humidity (RH) were recorded at 10 cm from the top of the canopy using the porometer immediately prior to collect samples for hydraulic measurements (see below). Air temperature and relative humidity were $30.2 \pm 0.7^\circ\text{C}$ and $44.2 \pm 5.9\%$, respectively with no statistically significant difference between the two irradiance levels ($n = 10$) in this regard.

2.3. Hydraulic measurements

In order to get an overall picture of the hydraulic map of the two genotypes under study, measurements of hydraulic conductance (K) were performed on five plants of each genotype at each irradiance level tested. The hydraulic conductance of whole plants and roots was measured using the 'evaporative flux' method (Nardini et al., 2003). In particular, hydraulic resistances of both whole plant ($R_{\text{plant}} = 1/K_{\text{plant}}$) and root ($R_{\text{root}} = 1/K_{\text{root}}$) were calculated on the basis of the Ohm's law hydraulic analogue as:

$$R_{\text{plant}} = \frac{(\psi_{\text{soil}} - \psi_{\text{min}})}{E_L}$$

$$R_{\text{root}} = \frac{(\psi_{\text{soil}} - \psi_x)}{E_L}$$

where E_L is the transpiration rate measured at midday and Ψ_{min} is the midday leaf water potential. The midday xylem water potential (Ψ_x) was estimated by measuring Ψ of leaves inserted near the base of plants that had been covered with plastic film and aluminium foil the evening preceding experiments. Soil water potential (Ψ_{soil}) was measured using a Dew Point Hygrometer (WP4, Decagon Devices, Pullman, WA, USA) on soil samples collected at different depths (50 and 120 cm). K_{plant} and K_{root} were then calculated as $K = 1/R$.

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