

Rootstock effects on xylem conduit dimensions and vulnerability to cavitation of *Olea europaea* L.

Patrizia Trifilò · Maria A. Lo Gullo ·
Andrea Nardini · Fulvio Pernice · Sebastiano Salleo

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Abstract Two clones of *Olea europaea* L. were studied for their potential impact on hydraulic architecture and vulnerability to xylem cavitation, when used as rootstocks. The clones used were ‘‘Leccino Minerva’’ (LM), showing vigorous growth and ‘‘Leccino Dwarf’’ (LD) with strongly reduced growth. Self-rooted LM and LD plants as well as their grafting combinations were compared, namely, LM/LD (Leccino Minerva grafted onto Leccino Dwarf rootstock) and LD/LM (Leccino Dwarf grafted onto Leccino Minerva rootstocks). Plants with LD roots (LD and LM/LD) showed significantly reduced leaf surface area compared with plants with LM roots. Xylem conduits of LD shoots were 25% more numerous than in LM shoots. When grafted onto LM rootstocks, however, LD shoots produced consistently wider and longer vessels than measured in LD self-rooted plants. This caused LD/LM plants to increase stem vulnerability to cavitation with threshold pressures for cavitation (P_c) of less than 0.5 MPa compared with LD self-rooted plants that had P_c of over 2.0 MPa. By contrast, although LD rootstocks caused some reduction of vessel diameter and length of LM scions, their influence on LM hydraulic architecture was too small to reduce vulnerability

to cavitation of LM scions with respect to that measured for LM self-rooted plants. Our conclusion is that although dwarfing rootstocks effectively reduce grafted plant size, they do not necessarily confer higher resistance to xylem cavitation to scions which would improve plant resistance to drought.

Keywords Olive · Grafting · Rootstock · Xylem architecture · Cavitation

Introduction

The use of rootstocks with different growth control potentials over the scion is a common practice in modern arboriculture. In fact, reduced vegetative growth is a desirable feature of fruit crops in the view of getting high-density orchards with reduced cultural costs associated with harvesting and pruning (e.g. Webster 1995; Tous et al. 1999). This is the reason why the study of the mechanisms responsible for rootstock effects on scion growth has received a great attention in the past and renewed interest in recent years (e.g. Beakbane 1956; Lockard and Schneider 1981; Kamboj et al. 1999; Lliso et al. 2004).

Several hypotheses have been advanced to explain the rootstock-mediated growth regulation. Some authors have suggested that reduced growth as induced by ‘dwarfing’ rootstocks may arise from altered water transport at the graft union (e.g. Soumelidou et al. 1994; Atkinson et al. 2003). Other studies have stressed the importance of altered plant water status as a factor, determining the vegetative growth of grafted trees (Berman and DeJong 1997; Cohen and Naor 2002; Basile et al. 2003a; Solari et al. 2006a). Additionally, nutritional and hormonal mechanisms have been proposed to explain the size-controlling potential of

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P. Trifilò · M. A. Lo Gullo
Dipartimento di Scienze Botaniche, Università di Messina,
Salita Sperone 31, 98166 Messina S. Agata, Italy

A. Nardini (✉) · S. Salleo
Dipartimento di Biologia, Università di Trieste,
Via L. Giorgieri 10, 34127 Trieste, Italy
e-mail: nardini@units.it

F. Pernice
Dipartimento di Colture Arboree, Università di Palermo,
V.le delle Scienze 11, 90128 Palermo, Italy

different rootstocks (Jones 1976; Richards et al. 1986; Sorce et al. 2002).

The recent introduction of innovative techniques like the high pressure flow meter (Tyree et al. 1995) has allowed to perform accurate measurements of the hydraulic properties of the rootstock, scion and graft union. The hydraulic conductance of the plant has been reported to be an important determinant of the growth potential of grafted plants of apple (Cohen and Naor 2002; Atkinson et al. 2003) but not of kiwifruit (Clearwater et al. 2004). Studies on peach (Basile et al. 2003b; Solari and DeJong 2006; Solari et al. 2006b) and olive (Nardini et al. 2006) have reported the scion growth to be largely influenced by the hydraulic conductance of the rootstock (K_r). As an example, K_r of dwarfing clones of olive was less than 50% that of vigorous ones (Nardini et al. 2006). In peach, the hydraulic conductance of the dwarfing rootstock 'K146-43' was approximately 10% that recorded for the more vigorous 'Nemaguard' rootstock (Solari et al. 2006b). In both cases, differences in K_r translated into marked differences in total leaf surface area and biomass partitioning.

Gas exchange rates, photosynthetic rates, growth and productivity of plants are largely determined by their hydraulic conductance (Ryan and Yoder 1997; Sperry 2000; Tyree 2003) as well as by the vulnerability of xylem to cavitation and embolism (Tyree and Sperry 1989; Salleo et al. 2000). In fact, trees tend to operate close to the critical water potentials triggering xylem cavitation due to their need to maximize gas exchange (Bond and Kavanagh 1999; Nardini and Salleo 2000; Meinzer 2002; Brodribb et al. 2003; Maherali et al. 2006). Hence, it can be predicted that the growth potential of grafted trees will be influenced by both plant native hydraulic conductance and by vulnerability of xylem to cavitation as changed as a consequence of grafting. To the best of our knowledge, no studies have appeared in the literature describing changes of vulnerability to cavitation of the scion as the result of grafting onto rootstocks with different vigour. A description of the differential resistance to water stress of apple trees grafted onto dwarfing or invigorating rootstocks has been reported by Oliën and Lasko (1986) and by Hussein and McFarland (1994) but the physiological basis of such differences remained unexplained. Other studies have reported the presence of smaller and/or fewer vessels in the roots and/or in the graft tissue of plants grafted onto low-vigour rootstocks (Simons 1986; Ussahatanonta and Simons 1988).

Vessel dimensions have been reported to be positively related to vulnerability to cavitation at least in one species (e.g. Lo Gullo et al. 1995). A thorough understanding of eventual variations of vulnerability to cavitation of grafted trees as a result of different scion/rootstock combinations would be especially useful in the case of orchards culti-

vated in semi-arid regions where drought stress represents an important limiting factor to plant growth. This is the case of olive trees growing in zones of the Mediterranean basin where summer rainfall is typically low and irrigation is an uncommon practice. The urgent need for innovative cultural practices in oliviculture has led to the development of clonal rootstocks with growth control potential over the scion (e.g. Baldoni and Fontanazza 1989; Pannelli et al. 1992; Rugini et al. 1996), but it is not clear whether different grafting combinations can effectively modify the resistance of olive plants to water stress. In this study, we report measurements of xylem conduit dimensions and vulnerability to cavitation of *Olea europaea* L. scions as grafted on clonal dwarfing and invigorating rootstocks.

Materials and methods

Plant material

All experiments were conducted on two different clones of *O. europaea* cv Leccino growing in an experimental field in Sciacca (Sicily, southern Italy, 37°30' 35" N, 13°04' 11" E). One clone was characterized by vigorous growth (Leccino 'Minerva', LM) while the second one showed strongly reduced vegetative growth (Leccino 'Dwarf', LD) (Rugini et al. 1996). Self-rooted (LM and LD) and grafted plants were studied. In particular, the graft combinations were LM/LD (LM scion grafted onto LD rootstock) and LD/LM (LD scion grafted onto LM rootstock). All plants were propagated in 2002 and grafted at the end of March 2004. Plants were grown in a greenhouse of the Department of Arboriculture, University of Palermo, until March 2005 when they were transplanted to 3000-l containers filled with a 3:2 (v/v) mixture of peat and fine pumice stone. 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 all the study periods.

Anatomical measurements

At the end of July 2005, current-year-twigs were collected early in the morning from five different plants per group and immediately fixed in FAA (formalin, acetic acid, ethanol, 1:1:1, v:v:v). Internodes from the proximal part of twigs were sampled and cross-sectioned using a microtome (mod. Cut 4055, SLEE Technick GmbH, Mainz, Germany). Sections were stained with 0.1% (w:v) safranin (staining in red lignified cell walls) and 1% (w:v) fast green (staining in blue-green cellulosic walls), and observed at 1,300× magnification under a microscope (Laborlux S,

Leitz GmbH, Stuttgart, Germany) connected to a PC via a digital camera (Leica Camera AG, Solm, Germany). The total number of conduits per section was counted and the inner diameters of conduits were measured using an image analysis software (Sigma Scan Pro 5.0). The potential cross-sectional conductive area was calculated as $\Sigma\pi r^2$ (where r is the inner conduit radius). On the basis of the measured vessel diameters, the efficiency of water transport per unit leaf surface area supplied was estimated in terms of $\Sigma\pi r^4/A_{L\ 1\text{-year-old}}$ where r is the conduit radius and $A_{L\ 1\text{-year-old}}$ is the leaf surface area supplied by the conduits upstream (measured using a leaf area meter, see below). At equal conditions of pressure, sap viscosity and sample length, in fact, $\Sigma\pi r^4$ is expected to be proportional to the flow density, according to the Hagen–Poiseuille equation.

Vessel lengths were measured using the technique reported by Sperry et al. (2005). Current-year twigs that had been measured for vulnerability to cavitation (see below) were first flushed with deionized water to remove emboli and then injected with silicone (Rhodorsil RTV-141, Rhodia, Cranbury, NJ, USA) mixed with a blue pigment (Pentaxol, Prochima, Pesaro, Italy) at $P = 0.5$ MPa for 3 h. Silicone hardening was complete after stems had remained in air for 24 h. Stems were then cut into serial 2-cm-long segments. Cross sections were prepared of stems using fresh razor blades and observed immediately under a microscope. The number of stained conduits was counted and referred to the total number of conduits per section. Vessel length distribution was then calculated using equations reported by Sperry et al. (2005).

Xylem vulnerability to cavitation

Vulnerability curves were measured on five current-year stems per group from five different plants, using the air-injection method (Lo Gullo and Salleo 1991; Cochard et al. 1992). Stems were 25 to 35 cm long. Stems were cut under deionized water and immediately connected to a hydraulic apparatus similar to that described by Lo Gullo and Salleo (1991). Native stem hydraulic conductivity (K) was measured at a pressure (P) of 8 kPa using 50 mM KCl solution filtered to 0.1 μm . Stems were then ‘flushed’ at $P = 175$ kPa for 20 min to remove emboli and the new hydraulic conductivity was re-measured at $P = 8$ kPa. The procedure was repeated until K became constant (K_{max}) which usually required two flushes. While twigs were still connected to the hydraulic apparatus, xylem embolism was experimentally induced using the air-injection technique consisting of clamping a pressure collar to the middle part of the stem (Tyree et al. 1999; Salleo et al. 2004) and applying air pressures of 0.5, 1.0, 1.5, 2.0, 2.5, 3.0 and 3.5 MPa, sequentially. Each pressure level tested was maintained for 10 min, and after each pressurization K was

measured at $P = 8$ kPa (K_p). The percentage loss of hydraulic conductivity (PLC) was computed as $\text{PLC} = [1 - (K_p/K_{\text{max}})] \times 100$. The highest level of air pressure tested was selected on the basis of preliminary measurements of leaf water potential isotherms (data not shown) showing that the leaf water potential at the turgor loss point (Ψ_{tlp}) of both LM and LD leaves was -3.28 ± 0.32 MPa ($n = 5$).

At the end of experiments, the total leaf surface area of the plants under investigation (A_L) was measured using a leaf area meter (LI-3000A, LiCor, Lincoln, NE, USA).

Statistics

Data were analyzed with SigmaStat 2.0 (SPSS, Chicago, IL, USA) statistics software. Differences between experimental groups were assessed by one-way analysis of variance (ANOVA). Post-hoc pairwise comparisons between all means were made with Tukey’s test.

Results

Whole-plant leaf surface area (A_L) differed markedly among the experimental groups (Table 1). Self-rooted LM plants had total leaf surface areas of about 1.06 m² while A_L of LD plants was only about 0.5 m². The specific rootstock used had a significant impact on A_L . In fact, when LM scions were grafted onto LD rootstocks, A_L was reduced to about 0.34 m², while LD scions grafted onto LM rootstocks developed a leaf surface area of about 0.72 m² which was not statistically different from the same variable recorded for LM self-rooted plants.

Vessel density of twigs from plants with LD roots was of the order of 540 and 450 conduits mm⁻² for LD and LM/LD plants, respectively, i.e. it was by 20 to 25% higher than the same variable measured in twigs with LM root systems (405 and 361 conduits mm⁻², respectively). By contrast, wood cross-sectional area of 1-year-old stems was significantly less in LD self-rooted plants (about 2.57 mm²) than that of LM-plants (about 3.5 mm²) which was, in turn, similar to that measured in both grafting combinations (Table 1).

The xylem conduit diameter distribution revealed that more than 65% of conduits of LM plants were ranging between 15 and 25 μm in diameter (Fig. 1a), whereas about 15% of conduits were less than 15 μm in diameter and about 18% of them were wider than 25 μm in diameter. Grafting LM scions onto LD rootstocks significantly increased the fraction of xylem conduits less than 15 μm in diameter (to about 28%) while a slight increase was only recorded for the fraction of conduits 30 to 35 μm in diameter. Twigs from LD self-rooted plants had significantly narrower conduits than LD/LM plants i.e. over 90%

Table 1 Total plant leaf surface area and vessel density measured in cross-sections of 1-year-old twigs of *O. europaea* (number of xylem conduits per unit cross-sectional wood area)

	Plant leaf surface area (m ²) (n = 5)	Vessel density (mm ⁻²) (n = 5)	Xylem cross sectional area of 1-year-old stem (mm ²) (n = 5)	$\Sigma\pi r^2$ (mm ²) (n = 5)	$\Sigma\pi r^4/A_L$ (e-12 mm ²) (n = 5)
LM	1.06 ± 0.18a	405 ± 77a	3.53 ± 0.56a	0.49 ± 0.09a	18.5 ± 3.2
LM/LD	0.34 ± 0.11b	361 ± 61a	3.47 ± 0.42a	0.45 ± 0.13a	24.2 ± 5.6
LD	0.50 ± 0.09b	540 ± 81b	2.57 ± 0.27b	0.32 ± 0.07b	19.8 ± 5.5
LD/LM	0.72 ± 0.22ab	450 ± 39b	3.68 ± 0.59a	0.64 ± 0.01c	25.1 ± 3.6

$\Sigma\pi r^2$ is the potentially conductive wood cross-sectional area and $\Sigma\pi r^4/A_L$ is a parameter set as proportional to the theoretical flow ($\Sigma\pi r^4$) normalized by the supplied leaf surface area (A_L). LM and LD are self-rooted plants of the ‘‘Leccino Minerva’’ clone and of the ‘‘Leccino Dwarf’’ clone, respectively. LM/LD were plants obtained by grafting LM onto LD rootstocks. LD/LM were plants with LD as scion and LM as rootstock. Means are given ± SD

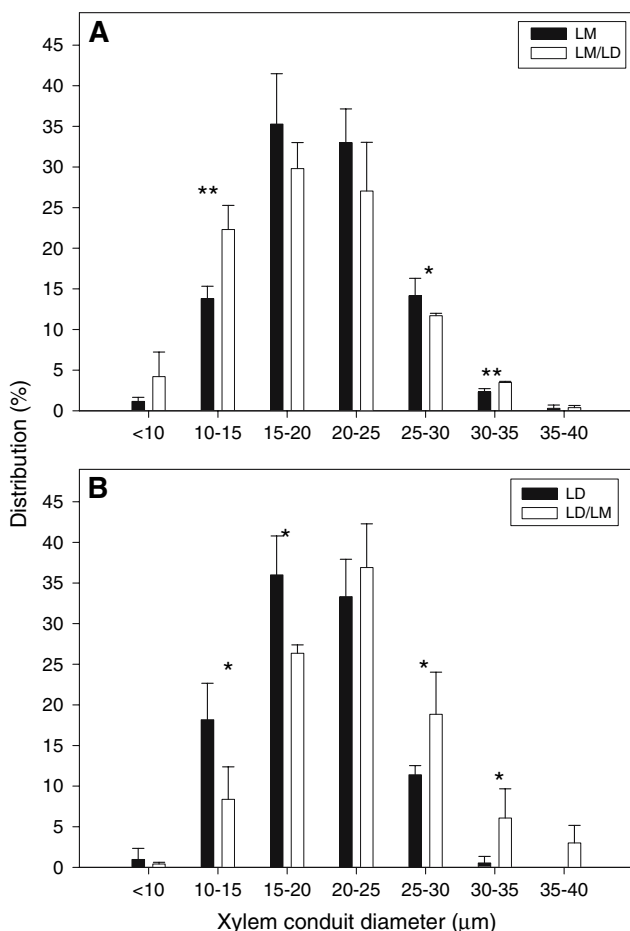


Fig. 1 Xylem conduit diameter distribution measured of 1-year-old twigs of *O. europaea* L. self-rooted clones (LM, LD) and of their grafting combinations (LM/LD and LD/LM). Abbreviations are as in Table 1. *Significance of the difference for $P < 0.05$. **Significance of the difference for $P < 0.01$. Vertical bars are SD of the mean (n = 5)

of conduits were less than 25 µm in diameter versus about 70% in twigs of LD/LM plants (Fig. 1b). Moreover, conduits wider than 25 µm were about 26% in twigs of

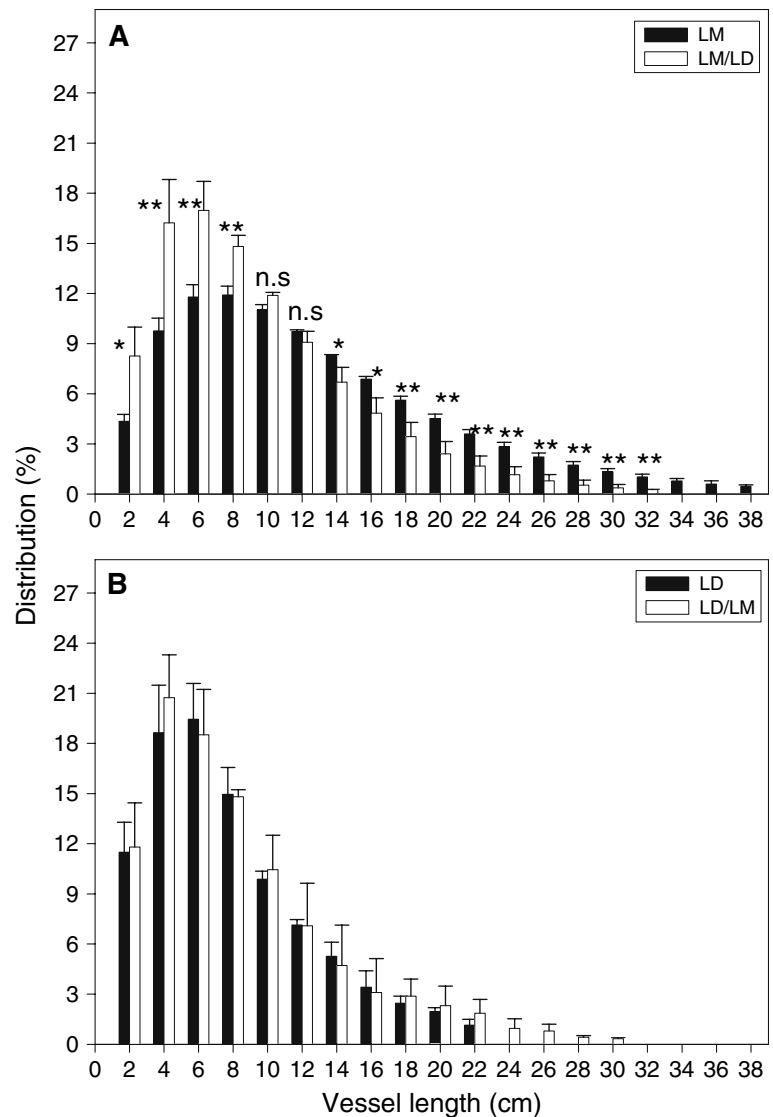
LD/LM plants versus only 12% in twigs of LD plants. Finally, it was noted that the widest conduits (35 to 40 µm in diameter) were only present in twigs of LM/LD plants.

Grafting LM scions onto LD rootstocks induced reduction in the mean vessel length of 1-year-old twigs (Fig. 2a), in that the fraction of conduits shorter than 10 cm increased as a consequence of grafting (from 55% to about 70%), while the fraction of conduits longer than 14 cm decreased significantly. Vessels as long as the twig i.e. longer than 32 cm were observed in LM plants but not in LM/LD ones. In contrast, grafting LD scions onto LM rootstocks did not induce differences in the vessel length distribution compared with self-rooted LD plants. The only difference between LD and LD/LM plants in this regard was the presence of vessels longer than 22 cm in the latter which were absent in the former.

The $\Sigma\pi r^4/A_L$ 1-year-old ratio did not differ statistically among the experimental groups tested (Table 1), suggesting that the unit photosynthetic area was, at least potentially, equally supplied with water and nutrients in self-rooted LD and LM plants as well as in their grafting combinations.

When tested for vulnerability to xylem cavitation, twigs of plants with LM shoot (LM and LM/LD, Fig. 3a) showed no loss of hydraulic conductivity up to applied air pressures (P) of 1.5 MPa. About 25% loss of conductivity was recorded in these plants at $P = 2.0$ MPa which increased up to about 45% at the highest pressure tested ($P = 3.5$ MPa). By contrast, LD plants showed significantly higher resistance to xylem cavitation, in that no loss of hydraulic conductivity was recorded up to $P = 2.0$ MPa, and even at $P = 3.5$ MPa their loss of hydraulic conductivity was less than 30% (Fig. 3b). The vulnerability to cavitation of twigs collected from LD scions grafted onto LM rootstocks was dramatically higher than that of LD self rooted plants. Here, 28% loss of hydraulic conductivity was recorded at $P = 0.5$ MPa, already and at $P = 2.0$ MPa this variable increased up to 40% and further to 60% at $P = 3.5$ MPa. In

Fig. 2 Xylem conduit length distribution measured of 1-year-old twigs of *O. europaea* L. self-rooted clones (LM, LD) and of their grafting combinations (LM/LD and LD/LM). Abbreviations are as in Table 1. *Significance of the difference for $P < 0.05$. **Significance of the difference for $P < 0.01$. Vertical bars are SD of the mean ($n = 5$)



other words, twigs from LD/LM plants were even more vulnerable to cavitation than those collected from self-rooted LM plants.

Discussion

Different graft combinations of invigorating with dwarfing olive clones differed in their impact on growth of young olive plants, in accordance with previous studies by some of us (Nardini et al. 2006). In particular, our present data describe the potential impact of grafting scions onto rootstocks with different vigour, on xylem architecture and vulnerability to cavitation of the shoot.

Self-rooted LD plants showed reduced vegetative growth when compared with LM ones in terms of total leaf surface area per plant (A_L) that was in the former about one

half that of the latter. In turn, LD and LM rootstocks confirmed to have an important growth control potential over the scion. In fact, dwarfing LD rootstocks induced vigorous LM scions to develop A_L which were not statistically different from those of self-rooted LD plants. By contrast, LM rootstocks proved to be effective in promoting increased vegetative growth of LD scions. Although the basic mechanism(s) for the different growth control potential of the rootstock is still not completely understood, plant hydraulics and more specifically root hydraulics have been suggested to play an important role in controlling plant growth in olive (Nardini et al. 2006).

The view that clonally produced dwarfing rootstocks possess innate features such as changes in xylem vessel anatomy which may explain their influence on shoot behaviour is not new (Beakbane and Thompson 1947; Atkinson et al. 2003). Accordingly, LD rootstocks induced

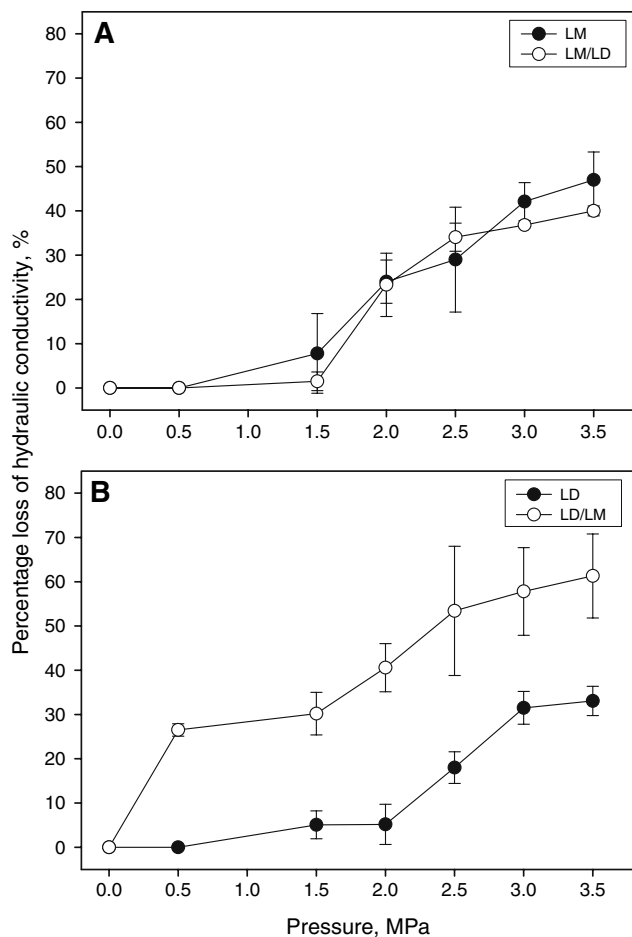


Fig. 3 Percentage loss of hydraulic conductivity measured of 1-year-old twigs of *O. europaea* L. self-rooted clones (LM, LD) and of their grafting combinations (LM/LD and LD/LM), after increasing air-pressurization. Abbreviations are as in Table 1. Vertical bars are SD of the mean ($n = 5$)

the production of shorter and narrower vessels in the twigs of vigorous LM clones compared with conduits of self-rooted LM plants. The opposite was true in the case of LD scions grafted onto LM rootstocks where wider and longer xylem conduits were produced in comparison with vessels typically observed in self rooted LD plants. It is worth noting that LD rootstocks induced the production of an almost double fraction of narrowest conduits (up to 15 μm in diameter) in LM scions compared with LM self-rooted plants. In contrast, LM rootstocks induced a consistent reduction in the percentage of narrow conduits of LD scions and production of large fractions of wide conduits (30 to 40 μm in diameter). The effect of LD and LM rootstocks on the conduit length distribution was very similar to that on conduit radii. Interestingly, LD shoots regardless if growing on LM rootstocks or on their own roots, had one-fourth to one-third more conduits per unit wood cross-sectional area (vessel density, Table 1) than LM shoots. In other words, LD roots apparently induced shoots to produce more

numerous xylem conduits which were, on average, shorter and narrower than in scions grafted on LM rootstocks. These two features of the olive water conducting system, i.e. number of conduits per unit wood cross-sectional area and conduit diameters did not influence, at least theoretically, the potential efficiency of the wood to supply leaves with water in that the $\Sigma\pi r^4/A_L$ 1-year-old ratio was not statistically different between the two graft combinations tested or between the two self-rooted clones (Table 1). Of course, this variable provides only a preliminary estimate of the actual wood efficiency per unit leaf surface area and we are aware that the Hagen–Poiseuille equation can be inadequate to quantify the xylem flow in some species (Giordano et al. 1978). However, it is of interest to note that the constancy of the computed $\Sigma\pi r^4/A_L$ 1-year-old ratio among the experimental groups, reinforces the view that plants tend to proportionate total transpiring surface area to xylem hydraulic efficiency in order to assure equal water supply to the unit photosynthetic area. Plant hydraulic architecture has been repeatedly reported to control leaf gas exchange and, hence, growth and productivity (e.g. Nardini and Salleo 2000). In our case, the dwarfing effect of the rootstock has shown to reside in changes in the xylem hydraulic architecture of the scion as induced by the LD rootstock.

It is generally agreed that vulnerability to cavitation of xylem conduits basically depends on the size of pit membrane pores through which microbubbles enter the conduits and nucleate sap cavitation (Tyree and Zimmermann 2002). In one species, a strong positive linear relationship has been reported to exist between vulnerability to cavitation and conduit diameter (Lo Gullo et al. 1995). Although this relationship appeared to be much weaker when referred to several species combined together, it has shown to still hold (Tyree et al. 1994). In our case, twigs of LM self-rooted plants were consistently more vulnerable to cavitation than those of LD plants (Fig. 3a, b) in accordance with the wider conduits in 1-year-old twigs of the former. In fact, the cavitation threshold of LD plants was recorded at applied air pressures of 2.0 versus 1.5 MPa as recorded for LM plants. Furthermore, at $P = 3.0$ MPa which corresponded to xylem tensions recorded in olive plants growing in semi-arid environments (Giorio et al. 1999), the loss of hydraulic conductivity of LM stems was over 40% versus only 25% for LD ones. Curiously, LM scions grafted onto LD rootstocks (LM/LD, Fig. 3a) showed the same vulnerability to cavitation as that recorded for LM self-rooted plants at all the air pressures applied, although stems of LM/LD plants had larger fractions of narrow conduits (up to 15 μm in diameter, Fig. 1a) than LM plants. It is possible that the recorded differences in the conduit diameter distribution were not large enough to cause significant changes in the overall stem vulnerability to cavitation. Our tentative conclusion, therefore, is

that the dwarfing rootstock (LD) was not effective in ameliorating the resistance of grafted plants to stem cavitation. By contrast, the use of the invigorating LM clone as rootstock caused a much stronger difference in the conduit diameter distribution of the LD scions, with consistently smaller fractions of narrow conduits (less than 20 μm in diameter, Fig. 1b) and even larger differences in terms of the fraction of conduits more than 25 μm in diameter. Conduits 30–40 μm in diameter were practically absent in LD plants but represented about 12% of total number of conduits in LD/LM plants. This can well explain the notable vulnerability to cavitation of LD scions when grafted on LM rootstocks. Here, a lowest cavitation threshold was measured of less than 0.5 MPa. It should be noted that Nardini et al. (2006) reported minimum Ψ_{leaf} of about –1.5 MPa for a subset of plants growing under the same conditions as those used in the present study. In other words, while intact LD plants were substantially more resistant to cavitation than LM ones, LD rootstocks failed to “transmit” this feature to LM scions whilst LM rootstocks induced enough modification in the hydraulic architecture of LD scions to make them even more vulnerable to cavitation as intact LM plants were. At present, we have no information of molecular mechanisms involved in the different capability of the two clones of influencing the xylem conduit geometry of the scions, when they are used as rootstocks. On the basis of the existing information, we can speculate that LM root systems may induce high auxin levels in the scions of the dwarfing clone which would explain wider xylem conduits developing in these scions in comparison to those of self-rooted LD plants. The opposite, however, did not occur for LD rootstocks and their influence on LM scions was rather scarce.

In conclusion, the common practice of grafting vigorous cultivars onto dwarfing ones with the aim of reducing plant size and possibly increasing their resistance to drought requires some caution and more detailed studies because plant size reduction is not a synonym of higher resistance to drought-induced cavitation and embolism. In contrast, vigorous rootstocks may induce, as in the case of olive, higher vulnerability to cavitation thus leading to the need of larger water volumes to prevent this potentially lethal condition.

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