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Are sclerophylls and malacophylls hydraulically different ?

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Abstract

This work tests the hypothesis that sclerophylls (*i.e.* hard-leaved species) would be less efficient than malacophylls (*i.e.* soft-leaved species) in terms of water transport through the stem as well as within the leaf blade. Mean leaf surface area (A_L), leaf specific mass (LSM) as well as shoot (K_{WL}), stem (K_{SL}) and leaf (K_{LL}) hydraulic conductances were measured in eight Mediterranean evergreen sclerophylls and eight temperate deciduous malacophylls. No difference was observed between the two groups in terms of K_{LL} and of the contribution of leaves to the overall shoot hydraulic resistance. Leaves represented in all cases 48 to 90 % of the shoot hydraulic resistance, suggesting that the sclerophyllous habitus does not *per se* lead to low efficiency in water transport within the leaf blade. A weak negative relationship ($r^2 = 0.252$) appeared to exist between K_{SL} and LSM. This might provide an explanation for the lower growth rates of sclerophylls with respect to malacophylls.

Additional key words: high pressure flow meter, leaf hydraulic conductance, leaf specific mass, shoot hydraulic conductance.

Introduction

Several studies (*e.g.* Grubb 1986, Salleo and Lo Gullo 1990, Turner 1994, Nardini *et al.* 1996, Salleo *et al.* 1997) deal with the possible functional role of sclerophylly, *i.e.* of the increased hardness of the leaf blade. This is usually caused by one or more of the following features: mesophyll compactness, mechanical cells, thick cuticle and thick outer epidermal cell walls (Cowling and Campbell 1983, Fahn 1990). A convincing body of evidence shows that leaf toughness and stiffness are not related in a simple way to leaf water relations, in contrast with the classical interpretation of sclerophylly of Mediterranean evergreens which understands it to be as an efficient adaptation to prevent excessive water loss (Seddon 1974, Mooney 1982).

Several aspects of the water relations of sclerophylls have been carefully investigated. In particular, measurements of pressure-volume curves and related parameters (Salleo and Lo Gullo 1990, Kyriakopoulos and Richter 1991, Salleo *et al.* 1997), of leaf water potential (Poole and Miller 1975, Acherar and Rambal 1992, Nardini *et al.* 1996), of transpiration (Lo Gullo and Salleo 1988, Rhizopoulou *et al.* 1991), and of leaf relative water content (Lo Gullo and Salleo 1988, Rhizopoulou and Mitrakos 1990, Salleo and Lo Gullo 1990) have been reported. Moreover, a number of ecological studies have investigated the relevant biochemical features of sclerophylls (*e.g.* Loveless 1962, Hevia *et al.* 1999, Poorter and De Jong 1999) as well as their bio-mechanical properties (*e.g.* fracture toughness) with relation to leaf life span and palatability to herbivores (*e.g.* Lucas and Pereira 1990, Turner 1994, Reich *et al.* 1998).

Little information is available in literature about the possible relationships between sclerophylly and leaf blade hydraulic conductance (K_L), *i.e.* the efficiency of water transport within the leaf blade. Rapid measurements of the hydraulic conductance ($K = 1/R$ where R is hydraulic resistance) of different plant organs

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Abbreviations: $\bar{A}_L$ - mean leaf surface area; DM - dry mass; HPFM - high pressure flow meter; K_L - leaf blade hydraulic conductance; K_{LL} - leaf blade hydraulic conductance scaled by leaf surface area; K_S - leafless stem hydraulic conductance; K_{SL} - leafless stem hydraulic conductance scaled by leaf surface area; K_W - leafy shoot hydraulic conductance; K_{WL} - leafy shoot hydraulic conductance scaled by leaf surface area; LSM - leaf specific mass; R - hydraulic resistance.

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have been recently made possible by the introduction of a novel instrument, the *High Pressure Flow Meter* (*HPFM*, Tyree *et al.* 1995). The *HPFM* has been used to measure the K_L of different woody species, especially of the genera *Quercus* and *Acer* (Tyree *et al.* 1993, Yang and Tyree 1994, Nardini and Tyree 1999, Nardini and Pitt 1999). These studies have shown that leaves can represent a significant percentage of the total hydraulic resistance of the shoot (up to 90 % in some *Quercus* species; Tyree *et al.* 1993, Nardini and Tyree 1999, Nardini and Pitt 1999).

The water transport in the leaf involves vascular as well as non-vascular pathways. The latter is likely to be represented by at least three different pathways: *a*) the apoplastic pathway by which water flows along the cell walls or through the air leaf fraction, *b*) the symplastic pathway, where water flows from one cell to the next one through plasmodesmata, and *c*) the transcellular pathway where water sequentially crosses cell (and eventually vacuole) membranes. The non-vascular hydraulic conductance, which is thought to be much lower than the vascular one (Tyree and Cheung 1977, Tyree and Yanoulis 1980, Yang and Tyree 1994), can be expected to depend on the overall length of the apoplastic pathway, on the number of cells that the water must pass through from the minor veins to the mesophyll air spaces, as well as on the permeability to water of the membranes (Tyree *et al.* 1999). So far, the different contributions of apoplastic and cell-to-cell water pathways to the overall hydraulic conductance have been studied in roots (*e.g.* Steudle and Peterson 1998), but little is known on the contribution of these two components to the total hydraulic conductance of the leaf blade.

On the basis of the information summarized above, typical sclerophylls might be expected to have lower K_L with respect to non-sclerophylls because of their anatomical leaf traits and in particular because of: *a*) a compact mesophyll that would force water to flow through an increased number of cells thus possibly increasing the overall length of the apoplastic pathway, and *b*) an increased number of lignified cells that might reduce mesophyll porosity and hence decrease the hydraulic conductance of the overall apoplastic pathway. In turn, low leaf hydraulic conductance might have many ecophysiological implications such as, for instance, reduced stomatal aperture and gas exchange rates (Sôber 1997, Tyree *et al.* 1999) or increased susceptibility to cavitation because of the very negative water potentials developing in the leaf veins under water stress conditions (Yang and Tyree 1994). It has also been suggested (Tyree and Yanoulis 1980, Salleo *et al.* 2000) that low leaf hydraulic conductance might represent a sort of "amplifier" of hydraulic signals leading to stomatal closure and control of cavitation.

A recent study by Tyree *et al.* (1999) suggested that no correlation exists between K_L and sclerophylly, expressed in terms of specific leaf area (SLA, *i.e.* the ratio of leaf surface area to dry mass), when different temperate and tropical species are compared. The present study was aimed at checking whether the sclerophylly of Mediterranean evergreens might lead to low leaf hydraulic conductance with respect to some non-sclerophyllous species which commonly grow in temperate climates.

Materials and methods

Plants: Experiments were performed on one-year-old shoots of eight evergreen sclerophylls (*Viburnum tinus* L., *Laurus nobilis* L., *Myrtus communis* L., *Phillyrea angustifolia* L., *Olea europea* L., *Quercus suber* L., *Quercus ilex* L.) and eight deciduous malacophylls (*Corylus avellana* L., *Malus domestica* Borkh., *Juglans regia* L., *Castanea sativa* L., *Cercis siliquastrum* L., *Magnolia soulangeana* Soul., *Calycanthus floridus* L., *Quercus robur* L.). The evergreen sclerophylls selected for the study are typical Mediterranean evergreens (Pignatti 1982), with the only exception of *Prunus laurocerasus* which is a commonly cultivated plant in Europe and has its original distribution area in Western Asia. Among the deciduous malacophylls, four (*C. avellana*, *J. regia*, *C. sativa*, *Q. robur*) are common temperate trees growing throughout Europe and the other four species (*M. domestica*, *C. siliquastrum*, *M. soulangeana*, *C. floridus*) are commonly cultivated trees (Fenaroli 1984).

All the species under study were represented by at least two adult plants per species, growing in the Botanical Garden of the University of Trieste (North-eastern Italy). All the experiments were performed in June and July 1999, *i.e.* when both evergreens and deciduous species had completed their current-year growth.

Measurements of mean leaf surface area ($\bar{A}_L$) and leaf specific mass (LSM): Mean leaf surface area ($\bar{A}_L$) and specific mass (LSM) were measured for at least 50 leaves per species collected from the southern exposed part of the crown. Leaves of the current year were collected in the field and transported to the laboratory (in plastic bags), where they were measured for surface area using a *Leaf Area Meter LI-3000A*, (*LI-COR*, Lincoln, USA). The leaves were then put in an oven at 70 °C for three days and weighed in order to obtain their dry mass (DM). Leaf specific mass (LSM) was calculated by dividing leaf DM by $\bar{A}_L$. In this form, LSM is equivalent to the "degree of sclerophylly" (DS) first introduced by Cowling and Campbell (1983). According to these authors, typical sclerophylls are characterized by DS (*i.e.* LSM) higher than 7.0 mg cm^{-2}.

Measurements of shoot and leaf hydraulic conductance: Shoot hydraulic conductance of at least five one-year-old shoots per species was measured using the *High Pressure Flow Meter* (*HPFM*). The *HPFM* was first developed by Tyree *et al.* (1993, 1995) and has since been employed to measure the hydraulic conductance of roots, shoots and leaves of different tree species (*e.g.* Tyree *et al.* 1993, 1995, 1998, Cochard *et al.* 1997, Nardini and Pitt 1999, Nardini and Tyree 1999). Briefly, the HPFM is an apparatus designed to perfuse distilled and filtered water into the base of a cut shoot (or a root system) while maintaining constant the pressure applied and measuring the corresponding flow.

Shoots from the south-exposed part of the crown were cut off early in the morning while immersed in water to prevent xylem embolism. They were transported to the laboratory and immediately connected to the HPFM. The pressure was increased to 0.3 MPa and the hydraulic conductance of the whole leafy shoot (K_W) was measured in the steady-state mode (see Tyree *et al.* 1995) *i.e.* measuring the flow at the pre-established pressure. After 20 to 30 min, the leaves appeared to be infiltrated with water and the flow became stable. K_W was calculated as the ratio between the recorded flow (F) and the pressure difference applied (ΔP). The leaf blades were removed and the new hydraulic conductance of the leafless stem (K_S) was re-measured. Because leaves can be considered as having conductances in series with stems (Tyree and Ewers 1991), the inverse conductances (= resistances) are additive in series, thus the leaf hydraulic conductance was calculated as the difference in resistance between leafy shoots and leafless stems (Tyree *et al.* 1999).

After each experiment, the total leaf surface area (ΣA_L) of the shoot was measured using a *Leaf Area Meter* (see above). K_W, K_S and K_L were normalized by dividing them by ΣA_L to obtain K_{WL}, K_{SL} and K_{LL} (Tyree *et al.* 1998).

Results

Leaf surface area ($\bar{A}_L$) and leaf specific mass (LSM): Evergreen sclerophylls displayed, on average, lower $\bar{A}_L$ with respect to deciduous malacophylls, with the only exception of *P. laurocerasus* ($\bar{A}_L$ = 87.8 cm^2) among the sclerophylls and *M. domestica* ($\bar{A}_L$ = 15.6 cm^2) among the malacophylls. In fact, mean $\bar{A}_L$ ranged between 3.4 and 11.8 cm^2 and between 32.0 and 63.2 cm^2 in sclerophylls and malacophylls, respectively (Fig. 1*A*).

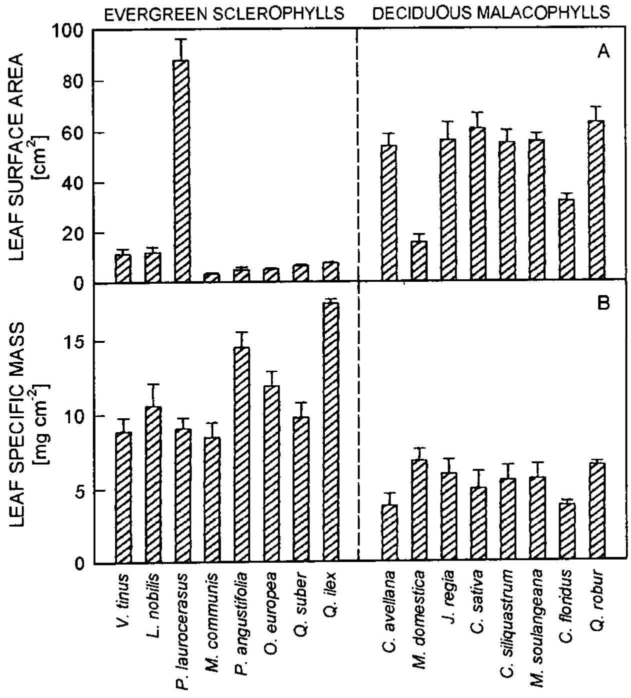

Fig. 1. Mean leaf surface (one side only) area (*A*), and leaf specific mass (*B*) as measured in eight evergreen sclerophylls and eight deciduous malacophylls. Means ± SD, *n* = 50.

As expected, mean leaf specific mass (LSM, Fig. 1*B*) was higher in evergreen sclerophylls (between 8.9 and 17.5 mg cm^{-2} for *V. tinus* and *Q. ilex*, respectively) than in deciduous malacophylls (between 3.9 and 6.9 mg cm^{-2}

for *C. avellana* and *M. domestica*, respectively). When the $\bar{A}_L$ of all the species studied was plotted *versus* the corresponding LSM, two distinct groups (with few exceptions) appeared to exist: one with species with LSM above 7.0 mg cm^{-2} and small leaf surface areas, and one with species with LSM below 7.0 mg cm^{-2} and high $\bar{A}_L$.

Shoot and leaf hydraulic conductance: No statistically significant difference could be recorded between evergreen sclerophylls and deciduous malacophylls in terms of K_{WL}. In fact, K_{WL} ranged between 0.027 and 0.167 g s^{-1} m^{-2} MPa^{-1} in evergreen sclerophylls and between 0.026 and 0.174 g s^{-1} m^{-2} MPa^{-1} in deciduous malacophylls (Fig. 2*A*). On the contrary, the K_{SL} of sclerophylls and of non-sclerophylls (Fig. 2*A*) seemed to be slightly different from one another, in that K_{SL} varied between 0.160 and 0.482 g s^{-1} m^{-2} MPa^{-1} in the evergreen species and between 0.172 and 0.605 g s^{-1} m^{-2} MPa^{-1} in deciduous trees (mean K_{SL} being 0.322 and 0.445 g s^{-1} m^{-2} MPa^{-1} for sclerophylls and non-sclerophylls, respectively). In all the species under study, large differences were measured between K_{WL} and K_{SL} (Fig. 2*A*), indicating that leaf blades account for a significant percentage of the total hydraulic resistance of the leafy shoot (see below). When K_{SL} was plotted *versus* LSM, however, a weak negative correlation appeared to exist between these two parameters ($r^2 = 0.252$).

No statistically significant difference could be found between sclerophylls and non-sclerophylls in terms of leaf blade hydraulic conductance, in that K_{LL} ranged from 0.028 to 0.369 and from 0.029 to 0.301 g s^{-1} m^{-2} MPa^{-1} in evergreen sclerophylls and deciduous malacophylls, respectively (Fig. 2*B*). When the K_{LL} of all the species studied was plotted *versus* the corresponding LSM, no correlation appeared to exist between the two variables.

In all the species under study, R_L represented more than 45 % of K_{WL} (Fig. 3). However, no difference could be detected between sclerophylls and non-sclerophylls, in this respect. In fact, R_L accounted for 47.1 to 94.3 % of K_{WL} in evergreen sclerophylls, and 53.1 to 90.3 % in deciduous malacophylls.

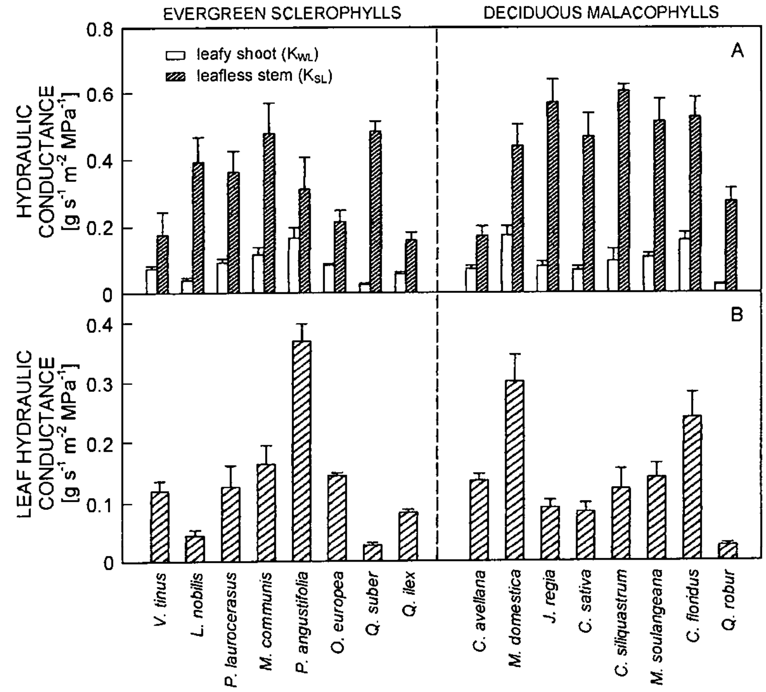

Fig. 2. Hydraulic conductance (scaled by leaf surface area) of leafy shoot, K_{WL} (*empty columns*) and leafless stems, K_{SL} (*dashed columns*) (*A*), and leaf blade hydraulic conductance scaled by leaf surface area, K_{LL} (*B*), as measured in eight evergreen sclerophylls and eight deciduous malacophylls using HPFM. Means ± SD, $n = 5$.

Discussion

Sclerophylly has been reported to be negatively correlated with leaf size (Grubb 1986, Turner 1994). This seems to be confirmed by this study since the Mediterranean evergreens considered showed higher LSM combined with lower $\bar{A}_L$, with respect to temperate trees. The only exception was *P. laurocerasus*. Reductions in leaf dimensions up to microphylly have been reported by Grubb (1986) in sclerophylls from different environments. This, might allow for the stomata to remain open while reducing the overall water loss by the plant. Reducing stomatal aperture, in fact, has negative consequences for CO_2 uptake.

The LSM value of 7.0 mg cm^{-2}, proposed by Cowling and Campbell (1983) to distinguish sclerophylls from non-sclerophylls, showed to be valid also in this case. However, this borderline LSM value appeared to have little or no physiological significance, as far as plant water relations are concerned. In the past, many authors have tried to relate LSM (or DS) to different water relation parameters, without success. In the present study, LSM did not correlate to either K_{WL} or K_{LL}, and the correlation of LSM to K_{SL} was dubious. Nonetheless, evergreen sclerophylls, as a group, seemed to have lower K_{SL} with respect to deciduous malacophylls. In a recent paper, Nardini and Tyree (1999) speculated that the higher shoot hydraulic conductance exhibited by typical water demanding *Quercus* species with respect to those adapted to aridity, might relate to growth potential and competitivity for light and soil resources. In particular, it was suggested that the success of species in mesic sites may depend on rapid growth, which would be promoted by high K_{SL}. On the contrary, in arid environments where growth is mainly limited by water availability, the ability to tolerate drought might be more crucial than the ability to transport water rapidly. Hence, arid zone plants need to invest less carbon into shoot conductance and thus, have lower K_{SL}. A similar pattern has been reported by Willigen and Pammenter (1998) in clones of *Eucalyptus*. Several recent studies show that photosynthesis (and hence growth and productivity) is closely related to plant hydraulic conductance (Ryan and Yoder 1997, Hubbard *et al.* 1999). Evergreen sclerophylls have been reported to have a slower leaf growth (Salleo and Lo Gullo 1990, Miyazawa *et al.* 1998) than deciduous trees. The differences recorded in the present study between sclerophylls and non-sclerophylls in terms of K_{SL}, might provide an interpretation of the different growth rates observed in the two groups, but further research is needed to better understand the role of shoot hydraulic conductance in determining the growth potential of plants.

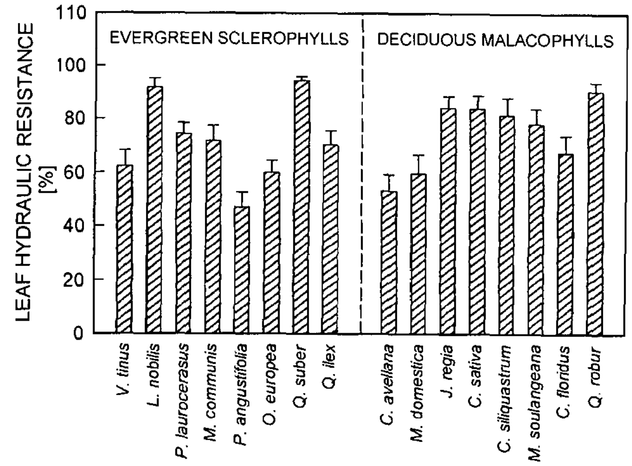

Fig. 3. Leaf hydraulic resistance (R_{LL}) of eight evergreen sclerophylls and eight deciduous malacophylls, expressed as a percentage of leafy shoot hydraulic resistance (R_{WL}). Means ± SD, $n = 5$.

The leaf blade represented a significant hydraulic bottleneck in all the species studied, regardless of their leaf habitus. In fact, R_L accounted for 48 to 92 % of the total hydraulic resistance of the leafy shoot. This result is in accordance with previous studies (Yang and Tyree 1994, Tyree *et al.* 1999, Nardini and Tyree 1999, Nardini and Pitt 1999) and suggests that leaf hydraulic resistance is usually high in woody plants. The leaf blade hydraulic conductance (K_{LL}) measured in the 16 species studied, varied between 0.028 and 0.369 g s^{-1} m^{-2} MPa^{-1}, which is in the same range previously reported by Tyree *et al.* (1993, 1999) for different tropical and temperate woody species. The results of the present study further broaden the range of K_L values reported for woody plants confirming that substantial water potential gradients are likely to develop within the leaf blade during transpiration (Yang and Tyree 1994). Assuming the transpiration rates to be 0.035 to 0.145 g s^{-1} m^{-2} (Nardini and Salleo, unpublished data), water potential drops of about 0.1 to 5.0 MPa might be expected between the base of the leaf and the mesophyll air spaces. Water potential gradients of such an order of magnitude might cause stomatal closure under water stress conditions. In particular, even small reductions of water flow, caused for example by cavitation in the stem and/or in the leaf veins, might result in large water potential drops within the leaf. These might be sensed by the stomata guard cells which would close to prevent further cavitation leading to runaway embolism. This is likely to represent an important mechanism in the well known phenomenon of stomatal control of cavitation (Jones and Sutherland 1991).

The hypothesis advanced that sclerophylly leads to low K_{LL}, was not verified because no relationship appeared to exist between K_{LL} and LSM. This finding would confirm previous considerations by Tyree *et al.* (1999) but leaves unanswered the question of how K_{LL} relates to leaf anatomy. A recent study has described the contribution of different leaf anatomical compartments to the overall leaf hydraulic conductance in *Festuca arundinacea* Schreb. cv. Clarine (Martre *et al.* 2000) but the ecophysiological significance of K_{LL} in the whole-plant hydraulic conductance still needs to be clarified.

In conclusion, sclerophylls and malacophylls are apparently not different from one another in terms of hydraulic efficiency of their leaves. Such differences seem somewhat more evident when species with different ecological adaptations are compared, regardless of their leaf habitus. It is possible that the functional significance of sclerophylly, if any, is related to the increased life-span of hard and coriaceous leaves (Reich *et al.* 1998). Simply, the search for correlations between sclerophylly and water relation parameters has to be abandoned in favour of a more promising interpretation of the functional role of this leaf trait.

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