Original article

Water relations and hydraulic characteristics of three woody species co-occurring in the same habitat

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Abstract – Three woody species typically encroaching the Karstic region of Trieste (Northeastern Italy) i.e. *Cotinus coggygria* L., *Prunus mahaleb* L. and *Fraxinus ornus* L., have been measured for diurnal and seasonal time courses of leaf conductance to water vapour, transpiration and water potential (Ψ_L), as well as whole-plant, shoot and root hydraulic resistance (R_{plant}, R_{shoot} and R_{root}, respectively) in view of investigating the impact of plant hydraulics on water stress resistance. *F. ornus* suffered the highest Ψ_L drop in July and September due to the high R_{plant} measured in this species. Positive significant relations were found of R_{plant} and Ψ_L to R_{root} in all three species studied, thus suggesting that root hydraulics is a major determinant of plant hydraulics and water stress resistance. The increasing R_{root} (and R_{plant}) from *C. coggygria* to *P. mahaleb* to *F. ornus* provided a possible explanation for the typical temporal sequence of expansion of the three species into degraded areas.

hydraulic architecture / water relations / *Cotinus coggygria* / *Prunus mahaleb* / *Fraxinus ornus*

Resumé – **Relations hydriques et caractéristiques hydrauliques de trois espèces ligneuses présentes dans le même habitat.** Trois espèces ligneuses, typiquement en cours d'extension dans la région Karstique de Trieste (Italie du nord) i.e. *Cotinus coggygria* L., *Prunus mahaleb* L. and *Fraxinus ornus* L., ont été suivies aux échelles journalières et saisonnières en termes de conductance foliaire pour la vapeur d'eau, de transpiration et de potentiel hydrique (Ψ_L), ainsi que de résistance hydraulique totale, tige et racinaire (R_{plant}, R_{shoot} and R_{root}, respectivement) dans l'objectif d'analyser l'impact des paramètres hydrauliques des plantes sur leur résistance au stress hydrique. *F. ornus* a montré la plus grande chute de Ψ_L en Juillet et Septembre en raison de la grande valeur de R_{plant} mesurée chez cette espèce. Des relations positives et significatives ont été trouvées entre R_{plant}, Ψ_L et R_{root} pour les trois espèces étudiées, ce qui suggère que les propriétés hydrauliques des racines sont un déterminant majeur des propriétés hydrauliques de la plante et de leur résistance au stress hydrique. Les valeurs croissantes de R_{root} (et R_{plant}) de *C. coggygria* à *P. mahaleb* et *F. ornus* fournissent une explication possible pour la séquence temporelle d'expansion de ces trois espèces dans les zones dégradées.

architecture hydraulique / relations hydriques / *Cotinus coggygria* / *Prunus mahaleb* / *Fraxinus ornus*

1. INTRODUCTION

The concept of "hydraulic architecture" of plants was first introduced by M. Zimmermann [43, 46] in view of relating the structure and physical properties of the water conducting system to plant water balance and adaptation to the environment. In this framework, the partitioning of the hydraulic resistances (R) along the plant body and their seasonal changes are of particular interest and, in fact, Zimmermann and co-workers have discussed extensively the possible evolutive and adaptive significance of changes in the hydraulic conductance ($K = 1/R$) of stems and leaves of several tree species [45, 46]. During the last two decades, our knowledge of the hydraulic architecture of plants has been enriched with accurate measurements of the hydraulic resistance of the root (R_{root}) whose dominant component (by

85 to 95%) has revealed to reside in the radial pathway between the soil and the root stele [16, 36]. In turn, the overall shoot resistance (R_{shoot}) has been reported to be dominantly located in the leaf blade (R_{leaf}) i.e. leaves would account for 50 to 90% of the measured R_{shoot} [19, 21, 40]. On the basis of the above, a plant might be viewed as consisting of two opposite poles i.e. the leaf and the radial soil-to-root stele pathway, both characterized by high R's and connected to one another by a low-R pathway (the xylem). This last water path, however, can increase its own R by a factor of two or more due to cavitation [41]. A convincing body of evidence, in fact, has accumulated showing that xylem cavitation takes place in conduits whenever tensions in them exceed critical thresholds so that gaseous microbubbles are sucked into conduits leading to their embolism and blockage [34, 41, 44]. Some of the several species studied for cavitation so far, however, have

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shown to recover from xylem embolism at least partly, as transpiration declines and even in presence of active transpiration [3] in a matter of minutes [8, 39] or hours [47].

According to the Ohm's law hydraulic analogue, the hydraulic resistance of a plant (R_{plant}) is positively related to the driving force for the flow corresponding to the water potential (Ψ) difference between the soil and leaf ($\Psi_{soil} - \Psi_L$) i.e.:

$$R_{plant} = (\Psi_{soil} - \Psi_L) / F, \qquad (1)$$

where F is the flow through the plant. Because the root and the shoot are serial components in a plant,

$$R_{plant} = R_{root} + R_{shoot}. \qquad (2)$$

Under sufficient water availability, the hydraulic resistance of the root is 50 to 60% of that of the whole plant [37] i.e.:

$$R_{root} \cong R_{shoot}. \qquad (3)$$

During water shortage conditions, however, as well as under freeze or salinity stress, R_{plant} can increase significantly in both its components (R_{root} and/or R_{shoot}, [4, 14, 16, 25]). In particular, R_{root} may increase due to root cavitation [11, 33] and/or to the new formation of a multi-layer suberized endoderm-like tissue that hydraulically isolates the stele from the cortex [5, 12, 16, 23]. In turn, R_{shoot} can be enhanced by stem and leaf vein cavitation [22, 28] and stomatal closure [30, 32]. Sperry et al. [31] have developed a model showing that plant water use is mainly limited by the efficiency of the xylem and only to a lesser extent by the rhizosphere. Nardini et al. [17, 20], on the other hand, reported that the decrease in leaf conductance to water vapour (g_L) and water potential (Ψ_L) recorded in *Quercus* species during Sicilian summers were paralleled by opposite changes in R_{root}. Now, the question arises whether the major contribution to the increase in R_{plant} under stress conditions is due to R_{root} or R_{shoot}. Answering this question has both theoretical and practical interest because the recovery of the hydraulic efficiency of the shoot i.e. xylem refilling and stomatal re-opening, is likely to require less metabolic investment by the plant than that of the root at least in the case new roots have to be produced to substitute for those no longer in hydraulic continuity with the soil [5, 12].

In view of investigating possible relationships existing between changes in hydraulic resistance of plants and their adaptation to the environment, in the present study we report daily and seasonal measurements of water relation parameters as well as of root and shoot hydraulic resistance in three field-growing species co-occurring in the same habitat i.e. *Cotinus coggygria* L. (Wig tree), *Prunus mahaleb* L. (Mahaleb cherry) and *Fraxinus ornus* L. (Manna ash). These species are dominant components of the vegetation developing during the natural encroachment of abandoned rural areas in the Karstic region (Friuli-Venezia Giulia, Northeastern Italy). The Karstic areas are characterized by high soil drainage [24] so that even in presence of sufficient annual rainfall, plants may suffer summer (and winter) water stress [20]. The dynamic sequence of expansion of the three species above into the area sees *C. coggygria* settling first, followed by *P. mahaleb* and some years later, by *F. ornus* [9, 10, 24]. A previous study of some of us [17] had shown that the co-occurrence of two

Mediterranean Quercus species (*Q. suber* L. and *Q. cerris* L.) in Sicily could be explained in terms of their complementary changes in R_{root} through the year that allowed the peaks of their water demand to be reached in different periods of the year. Therefore, a second objective of our study was to check whether the co-occurrence of *C. coggygria*, *P. mahaleb* and *F. ornus* might be explained on the basis of different hydraulics and adaptive strategies.

2. MATERIALS AND METHODS

2.1. The study site

The study site was located near the village of Basovizza in the Karstic area of Trieste at an altitude of about 300 m. The soil in this area is a poorly developed brown soil with rather low water retention [1, 24] and the typical climate has been defined as a pre-Alpine continental climate. Mean rainfall is about 1150 mm with a maximum in autumn and a minimum in winter (between January and March). Winter temperatures often fall below 0 °C and in the coldest month (January) the mean of the daily minima is, on average, 2.9 °C (data from the Oceanography and Meteorology Section, Dept. of Earth Sciences, University of Trieste). The vegetation in the study site consisted of well developed shrubs of *C. coggygria* mixed with *P. mahaleb* and *F. ornus* trees as dominant species. Other co-occurring woody species were: *Crataegus monogyna, Rosa canina, Q. pubescens, Acer monspessulanum, Juniperus communis* and *Pinus nigra* ([24] and personal observations).

2.2. Measurements of plant water status and hydraulics

The diurnal time course of leaf conductance to water vapour (g_L), transpiration rate (E_L) and water potential (Ψ_L) was recorded every 60 min between 0630 h (pre-dawn) and 1830 h solar time, in selected sunny days of May (23 to 25), July (26 to 28) and September (12 to 15) 2000. These months were selected for measurements because previous studies [18, 20] had shown that although the spring is usually rainy in Venezia Giulia, plants suffer some loss of hydraulic conductance due to winter embolism while July is the warmest month and September is usually preceded by a dry period (August) and coincides with the beginning of processes leading to leaf senescence. Measurements were performed on three adult individuals of each species with an estimated age of 15–20 years. The same individuals were measured for the above variables in May, July and September. Samples for measuring leaf water status and gas exchange (see below) were sun leaves collected from the S-exposed part of the crown.

Leaf conductance to water vapour and transpiration rate were measured of at least 15 leaves per species and per daytime using a portable steady-state porometer (LI1600, LiCor Inc., Lincoln, NE, USA). Air temperature (T_{air}), relative humidity (RH) and photosynthetically active radiation (PAR) were also recorded using the porometer cuvette, at about 1 m from the S-exposed part of the crown. Leaf water potential (Ψ_L) was measured of six to ten leaves per species and per daytime using a portable pressure chamber (3005 Plant Water Status Console, Soilmoisture Equipment Corp., Goleta, CA, USA) with sheets of wet filter paper inside the chamber to minimize water loss during measurements.

In order to estimate seasonal changes in Ψ_L at the turgor loss point (Ψ_{TLP}), pressure-volume curves [27, 38] of four to five leaves per species and per study period were measured. The turgor loss point served as a reference point for estimating the residual turgor of leaves

when reaching the minimum diurnal Ψ_L [13]. So as to quantify the overall diurnal drop in Ψ_L, the integral of Ψ_L was calculated between two reference daytimes i.e. predawn and sunset when Ψ_L is least negative. We named this variable "Water Stress Index" or WSI [42]. In other words:

$$WSI = \int_{t0}^{tx} \Psi_L(t)dt, \qquad (4)$$

where t_0 and t_x are predawn and sunset times, respectively and dt is the time interval during which Ψ_L was measured. This Ψ_L expression was first proposed by Mishio and Yokoi [15] and has proved to be a more reliable indicator of the amount of water stress suffered by plants [42] with respect to other common variables used to the same purpose like minimum Ψ_L or the difference between pre-dawn and minimum diurnal Ψ_L.

An estimate of the seasonal changes in the hydraulic resistance (R) of plants (R_{plant}) as well as of that of the root system (R_{root}) and shoot (R_{shoot}) was obtained using the "evaporative flux" method (EF) which is based upon the Ohm's law hydraulic analogue i.e.:

$$R_{plant} = (\Psi_{pd} - \Psi_{min})/ E_L, \qquad (5)$$

$$R_{root} = (\Psi_{pd} - \Psi_x)/ E_L, \qquad (6)$$

$$R_{shoot} = (\Psi_x - \Psi_{min})/ E_L, \qquad (7)$$

where Ψ_{pd} is pre-dawn Ψ_L which is assumed to equilibrate to soil water potential i.e. $\Psi_{soil} \approx \Psi_{pd}$ [26], Ψ_{min} is the minimum diurnal Ψ_L as measured at midday and E_L is the midday transpiration rate. The term Ψ_x represents the water potential of xylem at the trunk base. This was estimated by covering four to five leaves growing near the base of plants with plastic film and aluminum foil before sunrise. Under these conditions, leaf water potential is generally agreed to equilibrate to that of the adjacent xylem [26]. The covered leaves were collected at midday and measured for Ψ_L. Midday values of Ψ_L, Ψ_x and E_L were preferred because at this daytime plants are likely to have transpired all their stored water so that steady-state water flow conditions are likely to establish.

In other words, because Ψ_{pd} is assumed to equilibrate with Ψ_{soil} (which is the case for not really arid soils), $(\Psi_{pd} - \Psi_{min})$ in equation 5 would represent the water potential difference driving the flow from the soil to the leaf (at midday). In turn, $(\Psi_{pd} - \Psi_x)$ in equation 6 would be the driving force for the flow from the soil to the trunk base and $(\Psi_x - \Psi_{min})$ in equation 7 would be that between the trunk base and the leaf.

We are aware that in many cases Ψ_{pd} may not equilibrate with Ψ_{soil} [26], so that measuring Ψ_{soil}, directly would be more correct. However, Karstic soils are characterized by deep fissures in the rocky subsoil into which roots may penetrate, so that measuring the water potential of a soil sample is likely to provide false information of the water potential actually experienced by plant roots. In these cases, estimating Ψ_{soil} on the basis of Ψ_{pd} is preferable and Ψ_{pd} represents the maximum (i.e., least negative) water potential plants can reach under given conditions.

3. RESULTS

The annual time course of air temperatures (T_{air}) and precipitation (Fig. 1, data from the Oceanography and Meteorological Section, University of Trieste for the year 2000, recorded about 1 Km from the study site) was characterized by a typically arid and cold winter (mean T_{air} dropped to –6 °C and only about 10% of annual precipitation was recorded between January and March). Two peaks of
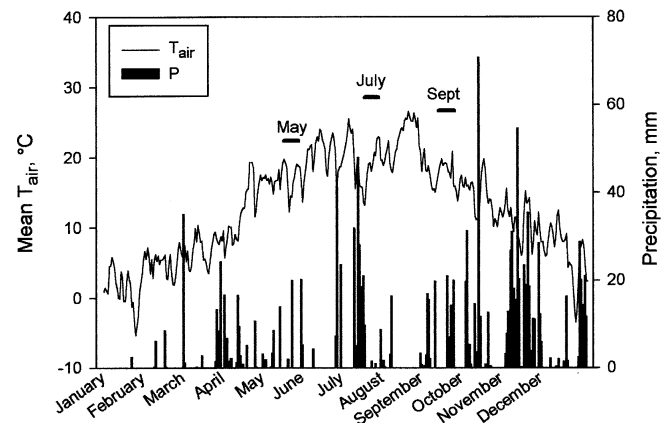

Figure 1. Annual time course of mean air temperatures (upper curve) and precipitation (vertical bars) during the year 2000. The study periods were May, July and September and are indicated by horizontal bars.

precipitation were recorded in the course of year 2000, one of which occurred in July i.e. about one month later with respect to the mean of the last 30 years, and a second one, in November. Therefore, measurements of plant water status in July were made during a warm, wet period. In September, on the contrary, plants received scarce rainfall (and in August as well, Fig. 1) while air temperatures were still high (mean T_{air} was over 20 °C).

3.1. Changes in plant water status

The diurnal time courses of g_L, E_L and Ψ_L as measured in the three species under study are reported in Figures 2, 3 and 4. Changes in g_L and E_L as recorded in May, July and September were qualitatively similar in *C. coggygria, P. mahaleb* and *F. ornus*, the largest midday g_L and E_L being recorded in July (g_L was 200 to 250 mmol m^{-2} s^{-1}) and the lowest values being recorded in September (g_L was 75 to 100 mmol m^{-2} s^{-1}). In all the three species and year periods studied, E_L paralleled g_L. The three species differed, however, for their Ψ_L time courses. In *C. coggygria*, Ψ_L decreased progressively from May to September (Fig. 2) both in terms of Ψ_{min} (from –1.0 to –2.0 MPa) and in terms of Ψ_{pd} (from –0.4 to –1.1 MPa). It can be noted, however, that the Ψ_L time course recorded in May was, in this species, not very different from that recorded in July.

The seasonal decrease in Ψ_L was slightly smaller in *P. mahaleb* with respect to that measured in *C. coggygria* in that Ψ_{min} decreased only from –1.2 to –1.8 MPa from May to September and Ψ_{pd} from –0.4 to –0.6 MPa in the same time interval. It has to be noted that the lowest diurnal Ψ_L values recorded in July in this species recovered promptly while they were maintained for several hours in September (from 0930 to 1600 h, Fig. 3) and recovered only during the night.

The diurnal time course of Ψ_L in *F. ornus* was quantitatively different from that recorded in the other two
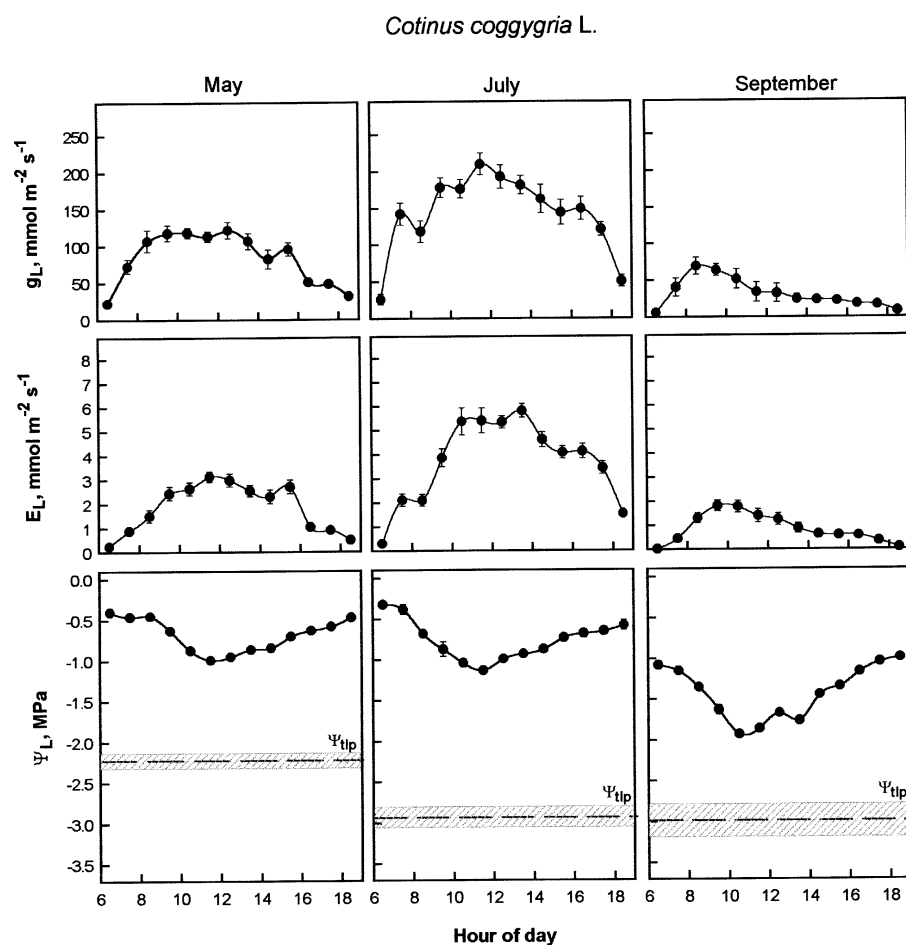
Cotinus coggygria L.

Figure 2. Diurnal time courses of leaf conductance to water vapour (g_L), transpiration (E_L) and water potential (Ψ_L) as measured in *Cotinus coggygria* L. field-growing plants. Vertical bars are SD of the mean. The mean leaf water potential at the turgor loss point (Ψ_{tlp}) is also reported ± SD (dashed area).

species (Fig. 4). The strong reduction in g_L and E_L (by a factor of over three) recorded in September with respect to values recorded in July, was paralleled by Ψ_L dropping to –3.5 MPa and reaching the turgor loss point (Ψ_{tlp}). Such a low Ψ_L level was more or less maintained during the warmest hours of the day i.e. between 1000 and 1600 h but it recovered in the afternoon. In the same month, also Ψ_{pd} was found to drop substantially i.e. it became threefold more negative than that recorded in May and July. Although July 2000 was characterized by unusually high precipitation (Fig. 1), Ψ_L of *F. ornus* dropped to –2.3 MPa, a level approaching the turgor loss point (Ψ_{tlp} was –2.5 MPa).

Figures 2, 3 and 4 show that the minimum diurnal Ψ_L values were either promptly recovered or maintained during the warmest hours of the day. In this last case, the total "pressure" acting on plant metabolism due to decreased water status can be better estimated in terms of WSI that takes into proper account the duration of the minimum Ψ_L levels and also the extent to which Ψ_{pd} actually decreased. WSI as calculated for *C. coggygria* and *P. mahaleb* was of the order of 8 to 9 MPa h for the former species and 12 to 14 MPa h for the latter in May and July, but increased significantly in

September when WSI increased twofold in *C. coggygria* i.e. from about 9 to 18 MPa h (Fig. 5). In *P. mahaleb*, meanwhile, the increase in WSI from the spring to late summer was of the order of only about 38% (from 13 to 18 MPa h). The largest changes in WSI were recorded in *F. ornus*, however, where the integral of Ψ_L between predawn and sunset increased significantly in July, already (from about 12 to 18 MPa h, i.e., by 50%) and much more in September when it was found to be of the order of about 35 MPa h i.e. three times higher than that calculated in May.

3.2. Partitioning of hydraulic resistances

Seasonal changes in R_{plant} and its components (R_{root} and R_{shoot}) are reported in Figure 6. The whole plant hydraulic resistance (R_{plant}, white columns) changed in a qualitatively similar way in the three species under study. In fact, R_{plant} was found to decrease in July with respect to May but to increase substantially in September. In the spring, the lowest R_{plant} was recorded in *C. coggygria* (about 1.0×10^4 MPa s m^2 kg^{-1}) and the highest one, in *F. ornus* (about double). R_{plant} as recorded in July was in every case, of the order of 20 to 30% less than

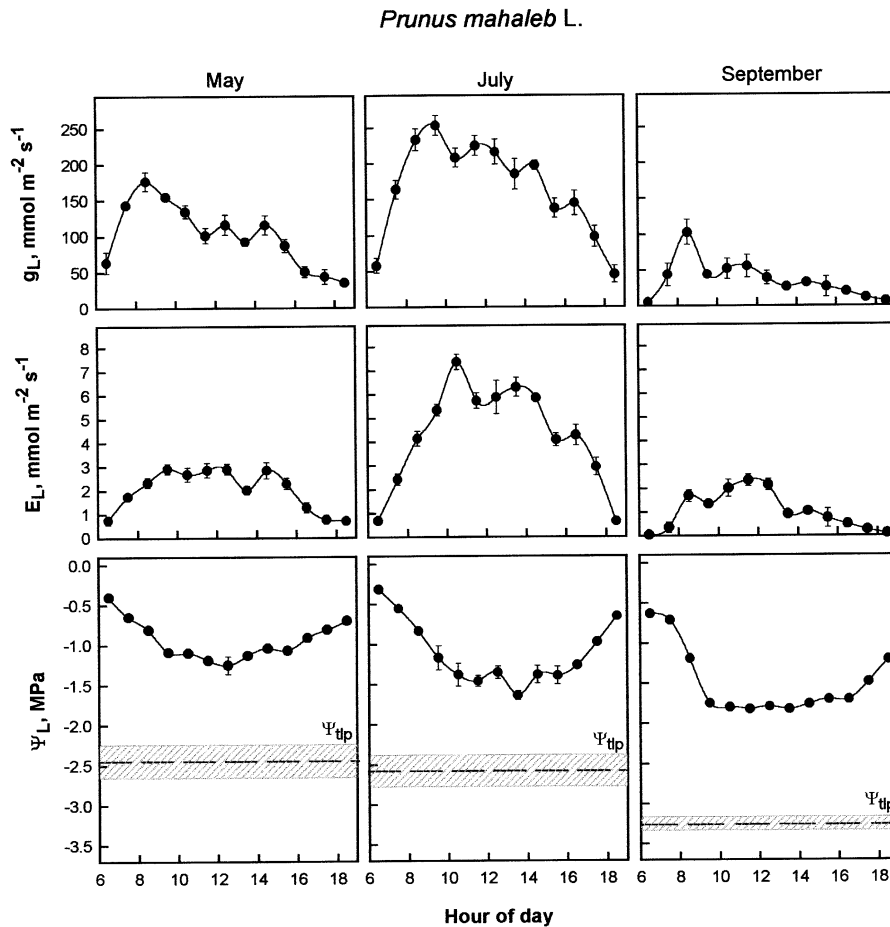## Prunus mahaleb L.

Figure 3. Diurnal time courses of leaf conductance to water vapour (g_L), transpiration (E_L) and water potential (Ψ_L) as measured in *Prunus mahaleb* L. field-growing plants. Vertical bars are SD of the mean. The mean leaf water potential at the turgor loss point (Ψ_{tlp}) is also reported ± SD (dashed area).

that measured in May. In September, R_{plant} was about twice as much as that measured in the spring in *C. coggygria* and *P. mahaleb* and 2.4 times more in *F. ornus*. In turn, R_{shoot} (dashed columns, Fig. 6) was significantly larger than R_{root} (black columns) in May, in all species studied. In July, the relative contribution of R_{shoot} to R_{plant} became smaller so that R_{shoot} became approximately equal to R_{root} in *C. coggygria* and *F. ornus* (about 0.25 and 0.8 × 10^4 MPa s m^2 kg^{-1}, respectively) while R_{shoot} was only about one third of R_{root} in *P. mahaleb* (R_{shoot} and R_{root} were about 0.2 and 0.7 × 10^4 MPa s m^2 kg^{-1}, respectively). In September, R_{shoot} contributed rather little to R_{plant} (only 10% in *P. mahaleb* and about one third in *C. coggygria* and *F. ornus*).

The impact of R_{root} on R_{plant} is described in Figure 7 where all R_{root} values recorded in the three species and year periods under study were plotted versus the corresponding R_{plant} values. The two variables resulted to be positively and linearly related to one another with a correlation coefficient as high as 0.91 and with a significance of $P < 0.0001$. The overall resistance of the root system (R_{root}) appeared to be also linearly and positively related to WSI (Fig. 8). The overall diurnal drop in Ψ_L (WSI) increased in response to the increase in R_{root}, in all species studied, with a coefficient of about 0.80 and a significance of $P < 0.01$.

4. DISCUSSION

The three species under study did not differ much for seasonal patterns of g_L, E_L or RWC (Figs. 2, 3 and 4). At least two significant differences among species, however, emerged in terms of seasonal changes in the Ψ_L time course. Primarily, diurnal Ψ_Ls recorded in *C. coggygria* and *P. mahaleb* did not approach their respective leaf turgor loss points in any of the periods studied i.e., leaves of the two species maintained their turgor even through the summer period. Leaves of *F. ornus*, meanwhile, not only showed Ψ_Ls dropping very near to their Ψ_{tlp} in July already but reached Ψ_{tlp} in September when leaf turgor was lost for several hours during the day (Fig. 4), in spite of consistent stomatal closure i.e., at low g_L. Secondly, the environmental pressure acting on plants, expressed here as the overall diurnal drop in Ψ_L (WSI, Fig. 5) was impressively high in *F. ornus* when compared to that estimated for the other two species (in July and September, WSI in *F. ornus* was about twice higher than that recorded for *C. coggygria*). Because the three species studied are deciduous and most trees in the study area initiate the processes leading to leaf senescence in late summer already [29], the lower leaf water status recorded in September with respect to May (and July) may be interpreted as the expression of the beginning of leaf senescence that has been reported to imply the loss of
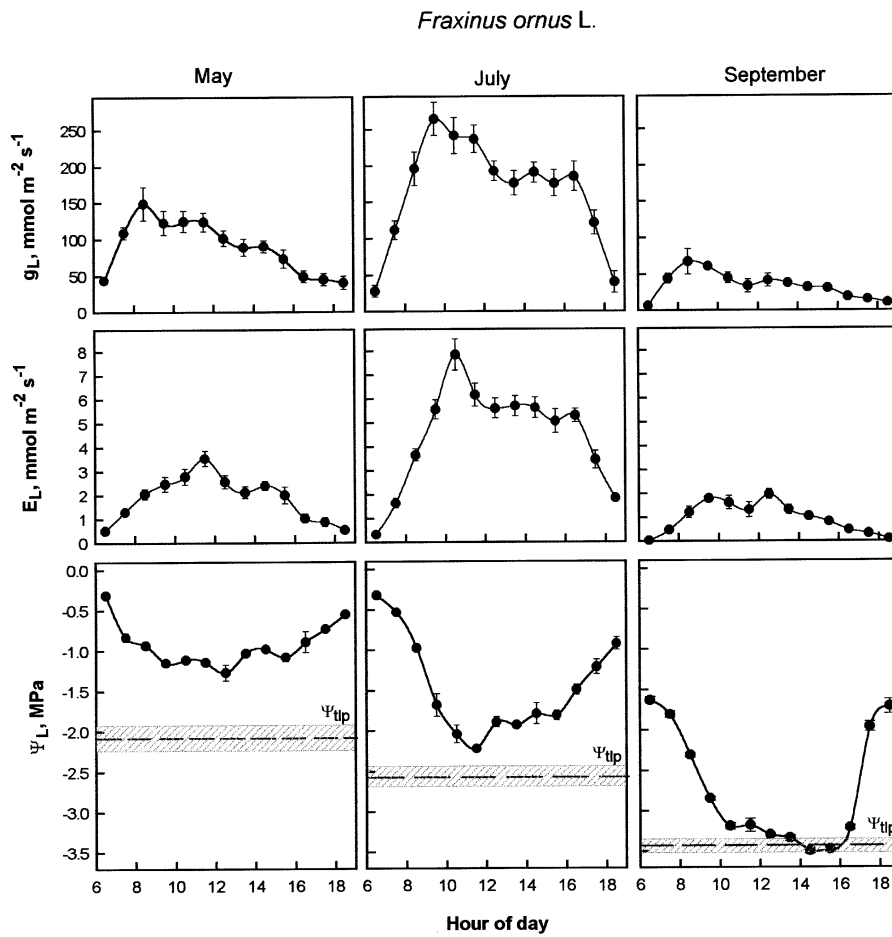
Fraxinus ornus L.

Figure 4. Diurnal time courses of leaf conductance to water vapour (g_L), transpiration (E_L) and water potential (Ψ_L) as measured in *Fraxinus ornus* L. field-growing plants. Vertical bars are SD of the mean. The mean leaf water potential at the turgor loss point (Ψ_{tlp}) is also reported ± SD (dashed area).
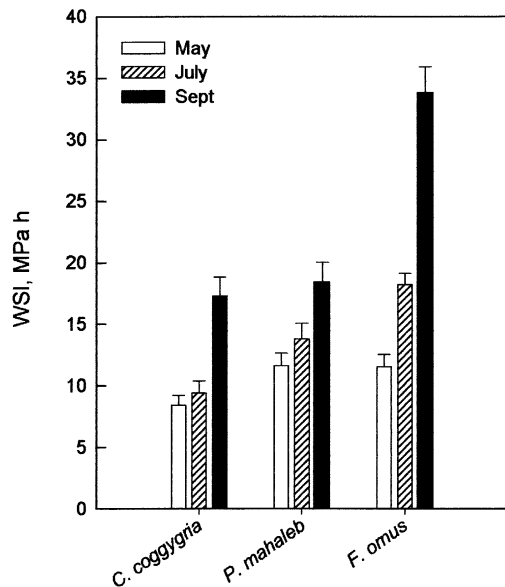

Figure 5. Integral of the diurnal time course of leaf water potential measured between predawn and sunset and here named "Water Stress Index" (WSI) calculated for the three periods under study in MPa h. Vertical bars are SD of the mean.

hydraulic efficiency of petioles and stems [29]. An alternative explanation, however, is that the Ψ_L drop recorded in September in all the species studied was the consequence of the water limitation suffered by plants in August when only 20 mm precipitation were recorded. In fact, water limitation accompanied by high temperatures (Fig. 1) is well known to lead to xylem embolism and impair of xylem water transport [33].

The overall plant hydraulic resistances (R_{plant}) were quite different in the three species studied (Fig. 6). In May, R_{plant} of *F. ornus* was twice as much as that recorded in *C. coggygria* and 25% more than R_{plant} of *P. mahaleb*. Such differences tended to increase in July and further in September when R_{plant} of *F. ornus* was 2.2 times more than that of *C. coggygria* and 58% more than that recorded in *P. mahaleb*. This suggests that differences in R_{plant} among species are dependent on their root, stem and leaf anatomy and they also depend on the ongoing functional losses by plant organs in terms of water transport efficiency. The decrease of R_{plant} recorded in July with respect to May in all the three species studied, was more due to the proportional decrease in R_{shoot} than to changes in R_{root} which changed not much (Fig. 6). In principle, R_{shoot} consists of the two serial components represented by stem and leaves i.e. $R_{shoot} = R_{stem} + R_{leaf}$. The hydraulic resistance of a stem can be expected to decrease as a consequence of cambial
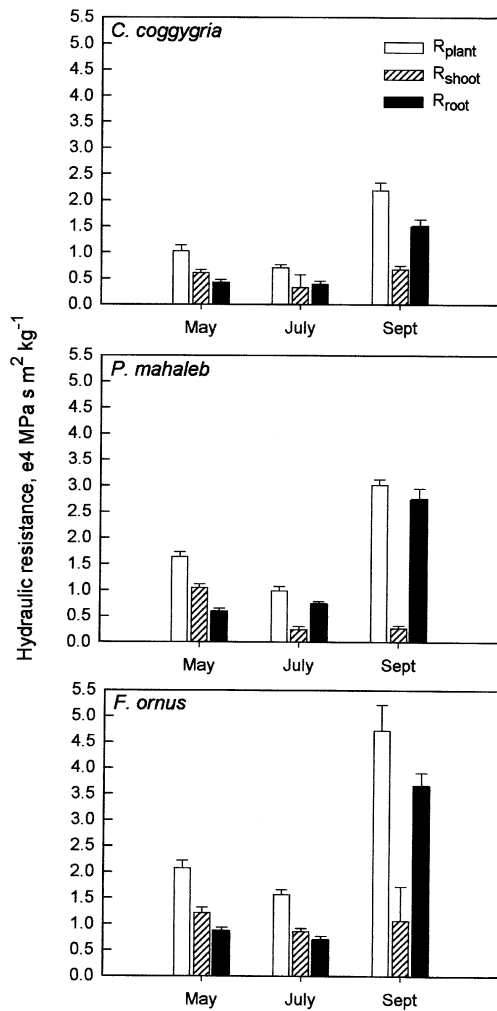
Figure 7. Relationship between the hydraulic resistance of whole plants (R_{plant}) and of roots (R_{root}). Different symbols indicate different species: *Cotinus coggygria* (open circles), *Prunus mahaleb* (solid circles), *Fraxinus ornus* (solid triangles). The centre solid line is the linear regression and the curved dotted lines are 95% confidence intervals. The coefficients of the straight line are reported together with the regression coefficient (r^2) and the P value (Pearson Product Moment Correlation).

Figure 6. Hydraulic resistance (R) of whole plants (R_{plant}, white columns), shoots (R_{shoot}, dashed columns) and roots (R_{root}, black columns) measured in the three periods and species under study. Vertical bars are SD of the mean.

Figure 8. Relationship between the integral of the diurnal time course of leaf water potential measured between predawn and sunset, here named "Water Stress Index" (WSI) and hydraulic resistance of roots (R_{root}). Different symbols indicate different species (see Fig. 7). The centre solid line is the linear regression and the curved dotted lines are 95% confidence intervals. The coefficients of the straight line are reported together with the regression coefficient (r^2) and the P value (Pearson Product Moment Correlation).

activity leading to the new production of wide conduits that contribute most to the flow [44] and, hence, to hydraulic conductance. In our opinion, the lower R_{shoot} recorded in July with respect to May can be interpreted as due to new xylem conduits produced between the end of May and July corresponding to the rhythm of stem growth reported by Barnett [2] and Evert [7]. Previous studies by some of us had provided evidence that loss of hydraulic conductance (PLC) of stems of some both deciduous and evergreen trees in Friuli Venezia Giulia was typically high in the winter, persisted partly in May and was recovered only in July. As an example, PLC measured in *Quercus pubescens* Willd. was as high as about 70% in May and dropped to 40% in July [18]. In *Quercus ilex* L., PLC was about 35% in May and 10% in July [20].
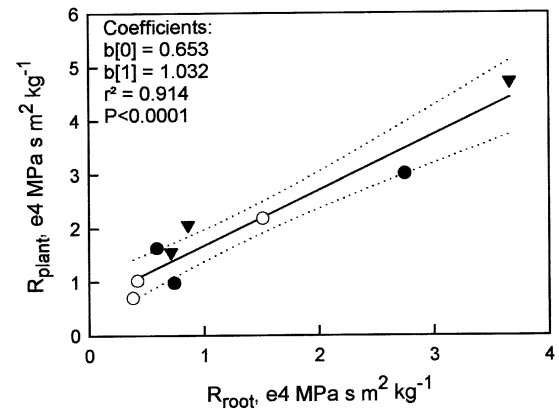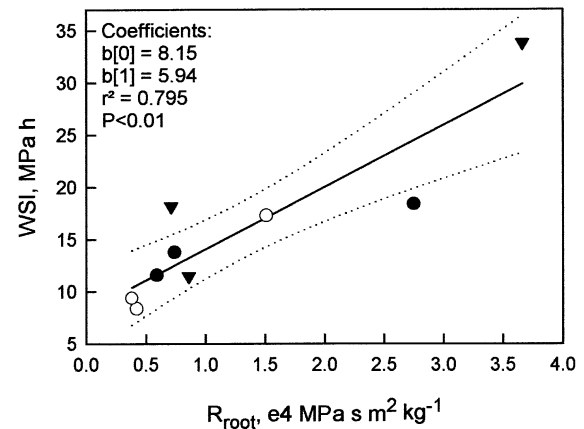
The noticeable increase in R_{plant} recorded in September for the three species under study was mostly due to R_{root} that represented 70 to 90% of R_{plant}. Several studies have reported consistent increases in R_{root} as a consequence of water stress [5, 12, 23] stimulating the new formation of an endoderm-like multilayer of suberized cells interrupting the hydraulic continuity between soil and the root stele [36]. The impressive increase in R_{root} in September provides, in our opinion, a good although circumstantial explanation for the significant

increase in WSI recorded in all the species studied, in the same month with respect to May as well as that recorded in *F. ornus* in July, already. Because R_{root} as derived on the basis of equation 6 includes the resistance of the soil-to-root pathway, it is possible that the measured R_{root} was due to the increase of R_{soil}. In turn, R_{soil} is negligible when soil water content and Ψ_{soil} are high. In our case, however, Ψ_{soil} as estimated on the basis of Ψ_{pd} was always below –0.3 MPa and as low as –1.6 MPa for *F. ornus* in September. This suggests that R_{soil} was not constant for the three species and for the three study periods. The differences recorded between species in terms of Ψ_{pd} also suggest that contrasting behaviors between species might be due to different rooting patterns. However, this is only a tentative explanation because we do not have any information about the rooting depth of the species studied. It has to be taken into account that this important aspect of plant adaptation is difficult to assess because of the extensive outcropping rocks typical of Karstic soils.

Over the entire study period, the whole-plant hydraulic resistance appeared to be strongly related to R_{root} (Fig. 7). The close correlation between the two, confirms the root as an organ highly sensitive to changes in environmental factors like temperature and water availability as well as to plant growth rhythms. This is in accordance with several recent studies attributing to roots a major role in determining the whole-plant water balance [6, 23, 35]. In our case, in fact, the diurnal drop in Ψ_L was related to R_{root} with a close correlation between the two variables. In this view, hydraulic measurements can significantly implement measurements of classic water relation parameters like Ψ_L, RWC and others and provide a more extensive understanding of their short-term and long-term changes.

The typical dynamic sequence of encroachment of abandoned grazing areas of the Karstic region [see above and 9, 10, 24] is in accordance with stress resistance strategies of the three species under study. In this regard, *C. coggygria* behaved like a drought resistant species combining high leaf gas exchange with rather low Ψ_L changes both in the spring and midsummer (Figs. 1 and 5). This was likely to be the result of constantly low R_{root}'s (less than 0.5×10^4 MPa s m^2 kg^{-1}) that allowed efficient water absorption and transport to leaves. Such highly efficient plant hydraulics might provide an explanation, in our opinion, of the rapid expansion of this species into abandoned degraded areas. We are aware that hydraulic architecture is only one of the factors which confer competitivity to pioneer species. Differences in height, leaf arrangement, crown shape, carbon allocation to roots versus leaves or root development, all are known to affect plant growth rate with respect to competitors. These factors were not taken into account in the present study, so our interpretation of the adaptive advantage of efficient plant hydraulics has to be taken as tentative. The significantly higher (about double) R_{root} and R_{shoot} recorded in *F. ornus* both in May and in July (Fig. 4) caused leaves of this species to approach turgor loss point during the warm period i.e. to make the species less competitive than *C. coggygria* (and *P. mahaleb*) for water and nutrient availability. The major vulnerability to water stress exhibited by *F. ornus* with respect to the other two species helps to explain why *F. ornus* expands into abandoned areas only border on newly encroached areas [24] where competition with other species is less critical and microclimatic factors are more favorable.

In conclusion, we feel that a more complete view of plant adaptation to the environment can emerge from a hydraulic description of plant organs which also allows to better interpret future possible trends in the restoration of degraded areas.

REFERENCES

[1] Abramo E., Michelutti G., Guida ai suoli forestali del Friuli-Venezia Giulia, Arti Grafiche Friulane, Udine, 1998.

[2] Barnett J.R., Reactivation of the cambium in *Aesculus hippocastanum* L. A transmission electron microscope study, Ann. Bot. 70 (1992) 169–177.

[3] Canny M.J., Vessel contents during transpiration – embolisms and refilling, Am. J. Bot. 84 (1997) 1223–1230.

[4] Cruz R.T., Jordan W.R., Drew M.C., Structural changes and associated reduction of hydraulic conductance in roots of *Sorghum bicolor* L. following exposure to water deficit, Plant Physiol. 99 (1992) 203–212.

[5] Dubrovsky J.G., North G.B., Nobel P.S., Root growth, developmental changes in the apex, and hydraulic conductivity for *Opuntia ficus-indica* during drought, New Phytol. 138 (1998) 75–82.

[6] Else M.A., Coupland D., Dutton L., Jackson M.B., Decreased root hydraulic conductivity reduces leaf water potential, initiates stomatal closure and slows leaf expansion in flooded plants of castor oil (*Ricinus communis*) despite diminished delivery of ABA from the roots to shoots in xylem sap, Physiol. Plant. 111 (2001) 46–54.

[7] Evert R.F., The cambium and seasonal development of the phloem in *Pyrus malus*, Am. J. Bot. 50 (1963) 149–159.

[8] Facette M.R., McCully M.E., Shane M.W., Canny M.J., Measurements of the time to refill embolized vessels, Plant Physiol. Biochem. 39 (2001) 59–66.

[9] Favretto D., Poldini L., Extinction time of a sample of Karst pastures due to encroachment, Ecol. Model. 33 (1985) 85–88.

[10] Feoli E., Feoli-Chiapella L., Ganis P., Sorge A., Spatial pattern analysis of abandoned grasslands of the Karst region by Trieste and Gorizia, Studia Geobot. 1 (1980) 213–221.

[11] Kavanagh K.L., Bond B.J., Aitken S.N., Gartner B.L., Knowe S., Shoot and root vulnerability to xylem cavitation in four populations of Douglas-fir seedlings, Tree Physiol. 19 (1999) 31–37.

[12] Lo Gullo M.A., Nardini A., Salleo S., Tyree M.T., Changes in root hydraulic conductance (K_R) of *Olea oleaster* seedlings following drought stress and irrigation, New Phytol. 140 (1998) 25–31.

[13] Lo Gullo M.A., Salleo S., Different strategies of drought resistance in three Mediterranean sclerophyllous trees growing in the same environmental conditions, New Phytol. 108 (1988) 267–276.

[14] Magnani F., Borghetti M., Interpretation of seasonal changes of xylem embolism and plant hydraulic resistance in *Fagus sylvatica*, Plant Cell Environ. 18 (1995) 689–696.

[15] Mishio M., Yokoi Y., A model for estimation of water flow resistance in soil-leaf pathway under dynamic conditions, J. Exp. Bot. 42 (1991) 541–546.

[16] Nardini A., Ghirardelli L., Salleo S., Vulnerability to freeze stress of seedlings of *Quercus ilex* L.: an ecological interpretation, Ann. Sci. For. 55 (1998) 553–565.

[17] Nardini A., Lo Gullo M.A., Salleo S., Competitive strategies for water availability in two Mediterranean *Quercus* species, Plant Cell Environ. 22 (1999) 109–116.

[18] Nardini A., Pitt F., Drought resistance of *Quercus pubescens* as a function of root hydraulic conductance, xylem embolism and hydraulic architecture, New Phytol. 143 (1999) 485–493.

[19] Nardini A., Salleo S., Limitation of stomatal conductance by hydraulic traits: sensing or preventing xylem cavitation? Trees 15 (2000) 14–24.

[20] Nardini A., Salleo S., Lo Gullo M.A., Pitt F., Different responses to drought and freeze stress of *Quercus ilex* L. growing along a latitudinal gradient, Plant Ecol. 148 (2000) 139–147.

[21] Nardini A., Tyree M.T., Root and shoot hydraulic conductance of seven *Quercus* species, Ann. For. Sci. 56 (1999) 371–377.

[22] Nardini A., Tyree M.T., Salleo S., Xylem cavitation in the leaf of *Prunus laurocerasus* L. and its impact on leaf hydraulics, Plant Physiol. 125 (2001) 1700–1709.

[23] North G.B., Nobel P.S., Drought-induced changes in hydraulic conductivity and structure in roots of *Ferocactus acanthodes* and *Opuntia ficus-indica*, New Phytol. 120 (1992) 9–19.

[24] Poldini L., La vegetazione del Carso isontino e triestino, Lint, Trieste, 1989.

[25] Prior L.D., Eamus D., Seasonal changes in hydraulic conductance, xylem embolism and leaf area in *Eucalyptus tetrodonta* and *Eucalytpus miniata* saplings in a north Australian savanna, Plant Cell Environ. 23 (2000) 955–965.

[26] Richter H., Water relations of plants in the field: some comments on the measurement of selected parameters, J. Exp. Bot. 48 (1997) 1–7.

[27] Salleo S., Water relations parameters of two Sicilian species of *Senecio* (Groundsel) measured by the pressure bomb, New Phytol. 95 (1983) 179–188.

[28] Salleo S., Lo Gullo M.A., Raimondo F., Nardini A., Vulnerability to cavitation of leaf minor veins: any impact on leaf gas exchange? Plant Cell Environ. 24 (2001) 851–859.

[29] Salleo S., Nardini A., Lo Gullo M.A., Ghirardelli L.A., Changes in stem and leaf hydraulics preceding leaf shedding in *Castanea sativa* L., Biol. Plant. 45 (2002) 227–234.

[30] Salleo S., Nardini A., Pitt F., Lo Gullo M.A., Xylem cavitation and hydraulic control of stomatal conductance in Laurel (*Laurus nobilis* L.), Plant Cell Environ. 23 (2000) 71–79.

[31] Sperry J.S., Adler F.R., Campbell G.S., Comstock J.P., Limitation of plant water use by rhizosphere and xylem conductance: results from a model, Plant Cell Environ. 21 (1998) 347–359.

[32] Sperry J.S., Alder N.N., Eastlack S.E., The effect of reduced hydraulic conductance on stomatal conductance and xylem cavitation, J. Exp. Bot. 44 (1993) 1075–1082.

[33] Sperry J.S., Ikeda T., Xylem cavitation in roots and stems of Douglas-fir and white fir, Tree Physiol. 17 (1997) 275–280.

[34] Sperry J.S., Tyree M.T., Mechanism of water stress-induced xylem embolism, Plant Physiol. 88 (1988) 581–587.

[35] Steudle E., Water uptake by plant roots: an integration of views, Plant Soil 226 (2000) 45–56.

[36] Steudle E., Peterson C.A., How does water get through roots? J. Exp. Bot. 49 (1998) 775–788.

[37] Tyree M.T., Ewers F.W., The hydraulic architecture of trees and other woody plants, New Phytol. 119 (1991) 345–360.

[38] Tyree M.T., Hammel H.T., The measurement of the turgor pressure and water relations of plants by the pressure-bomb technique, J. Exp. Bot. 23 (1972) 267–282.

[39] Tyree M.T., Salleo S., Nardini A., Lo Gullo M.A., Mosca R., Refilling of embolized vessels in young stems of laurel: do we need a new paradigm? Plant Physiol. 120 (1999) 11–21.

[40] Tyree M.T., Sinclair B., Lu P., Granier A., Whole shoot hydraulic resistance in *Quercus* species measured with a new high-pressure flowmeter, Ann. Sci. For. 50 (1993) 417–423.

[41] Tyree M.T., Sperry J.S., Vulnerability of xylem to cavitation and embolism, Annu. Rev. Plant Physiol. Mol. Biol. 40 (1989) 19–38.

[42] Vertovec M., Sakçali S., Ozturk M., Salleo S., Giacomich P., Feoli E., Nardini A., Diagnosing plant water status as a tool for quantifying water stress on a regional basis in Mediterranean drylands, Ann. For. Sci. 58 (2001) 113–125.

[43] Zimmermann M.H., Hydraulic architecture of some diffuse-porous trees, Can. J. Bot. 56 (1978) 2286–2295.

[44] Zimmermann M.H., Xylem structure and the ascent of sap, Springer Verlag, New York, 1983.

[45] Zimmermann M.H., Potter D., Vessel length distribution in branches, stem and roots of *Acer rubrum*, IAWA Bull. 3 (1982) 103–109.

[46] Zimmermann M.H., Sperry J.S., Anatomy of the palm *Raphis excelsa* IX. Xylem structure of the leaf insertion, J. Arnold Arbor. 46 (1983) 160–180.

[47] Zwieniecki M.J., Holbrook N.M., Diurnal variation in xylem hydraulic conductivity in white ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.) and red spruce (*Picea rubens* Sarg.), Plant Cell Environ. 21 (1998) 1173–1180.