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Original article

Whole shoot hydraulic resistance in *Quercus* species measured with a new high-pressure flowmeter

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Summary — Whole shoot resistance to water flow was measured in 4 species of oak, *Quercus robur* L, *Q petraea* Matt Liebl, *Q pubescens* Willd, and *Q rubra* L. Shoots were 1.1 to 1.5 m long with 16–19 mm basal wood diameter and were 4–8 yr old. Whole shoot resistances accounted for 20–40% of the total resistance to water flow from soils to leaves based on comparisons with literature values. Leaf blade resistances accounted for 80–90% of total shoot resistances measured in this study. Stem resistances to water flow were ≈ twice as large in *Q robur* than in the other species which had comparable stem resistances. Differences in shoot resistance between *Q robur versus Q petrae* are discussed in terms of the differential response of these species to drought in mixed stands.

***Quercus* / hydraulic resistance / water stress**

Résumé — Mesure de la résistance au transfert de l'eau chez différentes espèces de chênes au moyen d'un nouveau fluxmètre haute pression. *La résistance au transfert de l'eau de branches a été mesurée chez 4 espèces de chênes :* Quercus robur *L,* Q petraea *Matt Liebl,* Q pubescens *Willd et* Q rubra *L. Les branches avaient une longueur comprise entre 1,1 et 1,5 m, pour un diamètre de 16 à 19 mm à leur base, et étaient âgées de 4 à 8 ans. La comparaison des mesures avec des données de la littérature a montré que la résistance au transfert de l'eau dans les branches était de l'ordre de 20 à 40% de la résistance hydraulique totale, calculée entre le sol et les feuilles. La résistance au transfert dans les feuilles représentait de 80 à 90% de la résistance totale de la branche. Les résistances dans les parties ligneuses étaient environ deux fois plus élevées chez* Q robur *que chez les autres espèces, celle-ci montrant des valeurs comparables. Les différences de résistance hydraulique entre* Q robur *et* Q petraea *sont discutées en termes de différences de réponse à la sécheresse de ces espèces dans les peuplements mélangés.*

Quercus / *résistance hydraulique totale / résistance au transfert de l'eau*

INTRODUCTION

Some mid-European oak species are more sensitive to drought than others. Preliminary observations have shown that in mixed stands of *Quercus robur* and *Q petraea* only the former species was in decline following the exceptional drought that occurred in France in 1976 (Becker and Lévy, 1982). Another related species, *Q pubescens*, is mostly found in Southern Europe where severe drought develops every summer. So taxa of subgenus *Lepidobalanus* section *robur* (Krussmann, 1978), which includes all the above species, exhibit very different responses to water stress. Since 1976, a number of studies have been undertaken to determine the mechanisms of this difference in drought resistance but no striking differences have yet been found except for differences in vulnerability to cavitation, *Q robur* being more sensitive to drought-induced xylem dysfunction by cavitation than *Q petraea* which is as vulnerable as *Q pubescens* (Cochard *et al*, 1992).

Differences in hydraulic architecture of trees may contribute to their adaptation to drought (Zimmermann 1983; Tyree and Ewers 1991). The hydraulic resistance of the xylem of trees will determine, in part, the degree of water stress in leaves as measured by xylem pressure potential, ψ_{xp}. A reduced ψ_{xp} (more negative) can cause reduced cell expansion, wall synthesis, protein synthesis, stomatal conductance and photosynthesis and an increased xylem dysfunction by cavitation events. According to the soil–plant–atmosphere–continuum model of water flow in trees, the ψ_{xp} of leaves will be determined by the soil water potential, ψ_{soil}, the hydraulic resistances of the root and shoot (R_r and R_s, respectively) and the evaporative flux density from leaves, E, according to the following equation.

$$\psi_{xp} = \psi_{soil} - E\,(R_r + R_s) \qquad [1]$$

In this study, we have used a new high-pressure flowmeter to make rapid comparisons of the hydraulic architecture of shoots of 4 oak species (*Q robur, Q petraea, Q pubescens*, and *Q rubra*).

MATERIALS AND METHODS

Plant material

Branches of *Quercus robur, Q petraea, Q pubescens*, and *Q rubra* were collected from Champenoux, France (16 km east of Nancy) from the same trees as those used in the study of Cochard *et al* (1992). Branches ≈ 2 m long and 25 mm in diameter at the base were cut with pole pruners from the south side of mature trees in a sunny location. Within 5 min the branches were transported back to the laboratory where the base of the branch was placed under water and recut ≈ 0.3 m from the base to remove some of the air bubbles sucked into the stem during the initial cut.

Prior to connecting shoots to the high-pressure flowmeter described below, all cut surfaces were shaved with a razor blade to remove blockage of cut vessels by cell-wall fragments formed by the initial cuts.

The high-pressure flowmeter

The flowmeter shown in figure 1 permitted the perfusion of water into the base of a branched system while measuring the flow rate F (kg s^{-1}). The main body of the system was constructed from glass tubing, tygon tubing, stopcocks, and plastic T-junctions. Water was held in a flexible plastic bag inside a pressure reservoir (R). Water contained in the reservoir was distilled water filtered through an 0.1 μm filter. The water was placed under pressure by compressed air, controlled with a pressure regulator (PR) using gas from a compressed-air tank (not shown). The water was directed through a capillary tube (CT, 0.7 mm diameter and 0.12 m long) and then onto the shoot. The rate of flow, F, across the

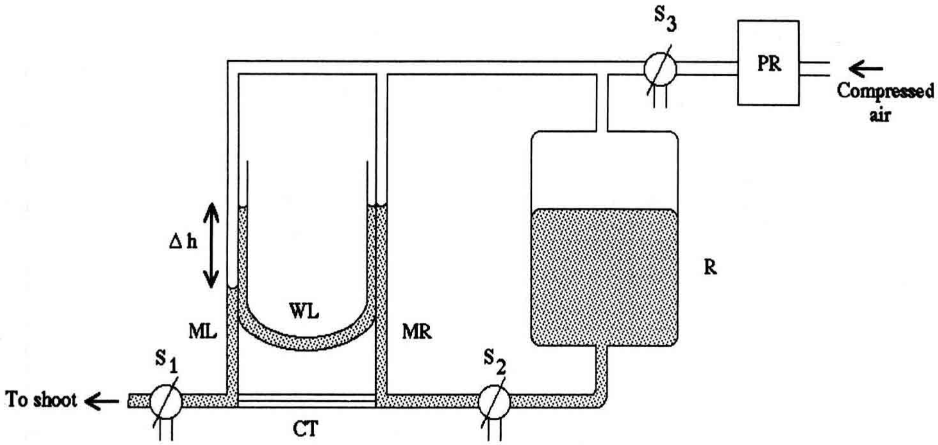

Fig 1. Diagrammatic representation of the high-pressure flowmeter. See text for details.

CT is proportional to the pressure drop across the tube; this pressure drop was recorded with a 2-arm water manometer system made from thick-walled glass capillary tubes of 1.5 mm internal diameter. The water level in the right arm of the manometer (MR) was always at the same level as the water in the reservoir (R). The same air pressure used to pressurize water in the reservoir (R) was transmitted to the top of the right and left manometer columns *via* lengths of tygon tubing. This prevented the water in the right arm of the manometer (MR) from rising above the level of water in the reservoir when the water was under pressure. The level of water in the left arm of the manometer (ML) depended on the rate and direction of flow across CT. Usually, flow was from right to left across CT (fig 1) and this made the level in ML below that in MR. To facilitate more accurate measurement of the height difference, Δh, between MR and ML, a water level (WL) was used to transfer the level of water from MR to ML. The WL consisted of a length of tygon tubing partly filled with water. The position of the tubing was adjusted so that the level of water in WL coincided with that in MR; the Δh could be measured at the place shown in figure 1. Three-way stopcocks (S_1 and S_2) were used to fill the flowmeter and reservoir with water and S_3 was used to release air pressure from the system.

The flowmeter was calibrated by directing flow of water across a length of stem segment *via* water-filled tubing to a container of water on a balance. Flow rate, F, was adjusted to different values by changing the air pressure in R and measuring the rate of flow (kg s^{-1}) into the container of water on the balance. Calibration curves were linear with a maximum deviation from the best fit straight line of 1.5% full scale. The difference in water levels, Δh, was rarely 0 at $F = 0$, because of differences in surface tension of water in MR and ML. The height difference at $F = 0$ was measured and subtracted from all readings (usually a correction of 1–3 mm). The problem of a non-zero Δh_0 could have been eliminated by replacing the manometer columns with a differential pressure gauge like that used in a low-pressure flow meter described by Tyree (1983). However, that would have eliminated the main advantages of the present high-pressure flow meter, *ie*, that it was inexpensive and could be used without a power source under field conditions.

Measurement of shoot resistances

Shoot resistances were measured by connecting the flowmeter to a shoot and perfusing water at 0.2 MPa pressure for 2 or 3 h. Initially, flow rate was high but declined gradually. The initially high flow rate was attributed to negative leaf water potentials, ψ_{leaf}. However, after 2 or 3 h the leaf air spaces were visibly infiltrated with water and water dripped from the stomata of some leaves and F became stable. Shoot resistance was computed from:

$$R_s = PA/F, \qquad [2]$$

where P was the applied water pressure, and A was the total leaf area of the shoots measured with a delta-T leaf area meter (Delta-T Devices Ltd, Cambridge, UK) at the end of the experiment. Normalization of R_s by multiplying P/F by A was justified because preliminary experiments revealed that large shoots (with large A) had smaller value of P/F than small shoots; see Yang and Tyree (1993) for a discussion of how P/F depends on branch size in *Acer saccharum*.

Resistances of the components of a shoot were measured by making resistance measurements after removal of each component. For example, the resistance of the whole shoot was measured before and after removal of leaf blades. Leaf-blade resistance was calculated from

$$R_{leaf\,blade} = R_s - R_{\text{shoot with leaves removed}} \qquad [3]$$

Subsequently, all petioles were removed, then all current-year shoots, then all 1-yr-old shoots, etc. Measurements of the branch resistance before and after each removal were used to calculate resistances of each component by difference. All values were normalized by multiplying P/F by A.

RESULTS

Shoot resistances of oak were measured on shoots 1.1–1.5 m long with leaf areas of 1.1 to 2.1 m^2 and basal diameters of 16–19 mm. The shoots ranged in age from 4–8 yr. Resistances of removed components are shown in figure 2A. Leaf blade resistances were > 20-fold that of any other component (*eg*, petioles, current-year shoots, 1-yr-old shoots etc). The leaf blade resistance of *Q pubescens* ($2.42 \pm 0.12 \times 10^4$ MPa s m^2 kg^{-1}) was significantly higher ($P = 0.05$) than that of the other species which were not significantly different from each other (1.82 ± 0.12, 1.89 ± 0.16, $2.04 \pm 0.07 \times 10^4$ for *Q petraea*, *Q robur*, and *Q rubra*, respectively). Petioles of *Q robur* were too small to remove sep-

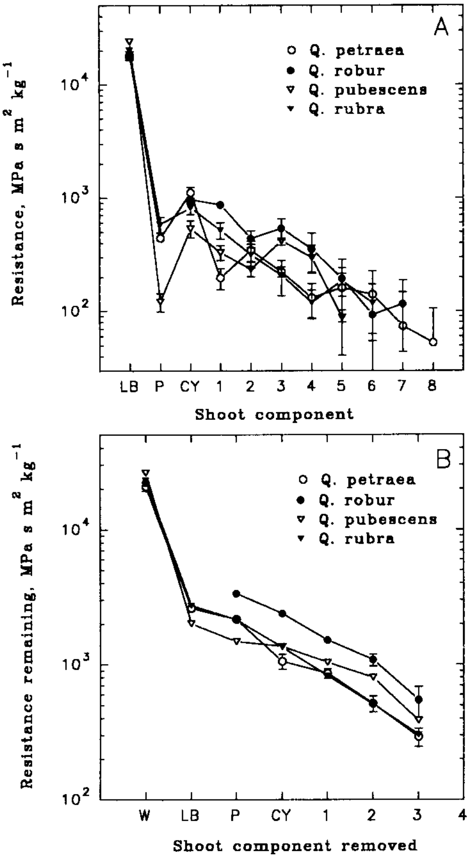

Fig 2. Shoot resistance of *Quercus* species. All points are means of 5 branches per species. Upper: Resistance of each component of the shoot. On the x-axis, LB: leaf blade; P: petiole; CY: current-year shoots; 1, 2, 3 etc refer to 1-, 2-, and 3-yr-old shoots respectively. Lower: shoot resistance values plotted as resistance remaining after removal of components. On the x-axis, W: whole shoot resistance with nothing removed; LB: resistance remaining after removal of leaf blades; P: resistance remaining after removal of leaf blades and petioles; CY: resistance remaining after removal of leaf blades, petioles and current year shoots; 1, 2 and 3 refer to resistance remaining after removal of everything including 1-, 2-, and 3-yr-old shoots respectively. Error bars are SEMs and are shown only when errors are larger than symbol size. In the lower graph representative error bars are shown only for *Q petraea* and *Q robur*.

arately, but the petiole resistances of all other species were significantly less than that from the current-year shoots. Petioles were removed by breaking them off from the current-year shoots. They broke near where the abscission zone would have formed in fall, but part of the vascular insertion zone would have remained behind in the current-year shoots. Our methods did not permit us to estimate the junction constrictions (if any were present) between the petioles and current-year shoots. There was a general trend of declining stem component resistance to water flow with increasing age of the stem.

In figure 2B the data are replotted to show the shoot resistance remaining after removal of each component labelled on the x-axis. "W" refers to the whole-shoot resistance (with leaves present). The resistance for "LB" refers to the resistance remaining after removal of leaf blades (petioles and all stems were still present). "P" refers to the resistance of the shoots after removal of the petioles (all stems were still present). The other notations on the x-axis have analogous meanings. The percentage of the whole shoot resistance remaining after removal of the leaf blades was 8.7 ± 0.3, 11.4 ± 1.6, 13.5 ± 1.5, and 18.5 ± 1.8 for *Q pubescens*, *Q rubra*, *Q petraea*, and *Q robur*, respectively. Thus, the leaf-blade resistances were 80–90% of the whole-shoot resistance.

DISCUSSION

The leaf-blade resistances of *Quercus* (1.87 to 2.4 x 10^4 MPa m^2 s kg^{-1}) are 2–4 times more than that which is found in other species where the values range from 0.5 to 1 x 10^4 MPa m^2 s kg^{-1} for *Fagus grandifolia* (Tyree and Cheung, 1977), *Juglans regia* (Tyree *et al*, 1993) and for *Acer saccharum* and *Populus deltoides* (Tyree and Alexander, unpublished data). The leaf-blade resistance includes vascular and nonvascular pathways from the base of the leaves to mesophyll airspaces, but we are of the opinion that the main resistance to water flow is probably in the nonvascular part of the path (Tyree and Cheung, 1977).

Leaf-blade resistances are relevant to a better understanding of stomatal physiology because they allow us to estimate gradient in water potential between minor veins and stomata, *ie*, leaf-blade resistances can be used to predict localized stomatal desiccation. Leaf blade resistances were very high when considered in terms of the water potential drop that would occur in them during normal transpiration. *Quercus* leaves have evaporative flux densities of 6 x 10^{-5} kg s^{-1} m^{-2} at midday (Bréda and Granier, unpublished data). Accordingly the drop in ψ from the base of the blade to mesophyll air spaces must be $E \bullet R_{\text{leaf blade}}$ = 0.87–1.45 MPa for *Q pubescens* and *Q petraea*, respectively, with the other 2 species within the above range. The resistances measured in this paper are probably about the same as or less than the resistance encountered by water during normal transpiration. The resistance to water flow in *Quercus* leaf blades could be higher during normal transpiration if most water evaporation occurs near the stomata in accordance with the evidence in support of peristomatal evaporation in substomatal cavities (Tyree and Yianoulis, 1980; Yianoulis and Tyree, 1984). The large resistance to water flow in leaves would cause a large reduction in the water potential of the guard cells of stomata and could account for the partial closure of stomata around midday observed in many *Quercus* species (Tenhunen *et al*, 1985; Epron *et al*, 1992).

One of the objectives of this study was to see if we could find further physiological evidence for *Q robur* being more in decline after drought episodes than *Q petraea*. *Q robur* is more vulnerable to cavitation than *Q petraea*, the former reaching 50% loss of the conductivity in petioles and current year stems at $\psi_{xp} = -2.7$ MPa whereas the latter did not reach 50% loss of conductivity until $\psi_{xp} = -3.3$ MPa (Cochard *et al*, 1992). Evaporative flux densities, *E*, are about the same for *Q robur* and *Q petraea*, but the shoot resistances to water flow are 1.5- to 2-fold higher in *Q robur* than in *Q petraea* (fig 3B). This difference in shoot resistance will tend to make stem ψ_s more negative in *Q robur* than in *Q petraea*. These differences in shoot resistance and in vulnerability to cavitation could make *Q robur* cavitate earlier in a drought cycle than *Q petraea*. However, it is difficult to say if the observed differences in shoot resistances of relatively small shoots in this study will have a dominating affect on field performance of the 2 species without further knowledge of root and bole resistances of the 2 species.

The shoot resistances we have measured are only a small fraction of the sum of the resistances in the soil, root, shoot and leaf of whole trees of *Quercus*. Whole tree resistances, R_{tree}, have been estimated for *Q robur* and *Q petraea* based on measures of predawn water potential (as an estimate of ψ_{soil}) and the relatioship between ψ_{leaf} and stem water flow under well-watered conditions. These R_{tree} values are in the range of 5 to 10 x 10^4 MPa s m^2 kg^{-1} and do not vary much with tree size (Cermak *et al*, 1980; Bréda *et al*, 1993; Simonin *et al*, 1993). Accordingly, the shoot resistance of this study accounts for about 20–40% of the resistance of the entire soil–plant hydraulic pathway. In a study on leafless shoots of *Acer saccharum*, ≈ 50% the total resistance to water flow in shoots 0.12 m in diameter at the base is contained in branches < 0.02 m basal diameter (Yang and Tyree, 1993). If the same pattern holds in *Quercus*, then we might predict that 30 or 50% of the total resistance to water flow is contained in the above-ground portion of trees with perhaps 80% of the shoot resistance contained in the leaf blades. The remainder of the whole tree resistance to water flow is accounted for by.roots and soil near the roots.

Studies have shown that R_{tree} increases by 400–500% as predawn ψ_s fall from 0 to –2 MPa (Bréda *et al*, 1993; Simonin *et al*, 1993) but that embolisms in small branches and petioles can account for only a 20 or 30% increase in resistance of small branches. It therefore seems unlikely that cavitation and differences in shoot resistance can account for all the observed changes in the hydraulics of whole trees during drought. How whole-tree resistances to water flow changes during drought, may be important for a better understanding of adaptation to drought.

However, differences in stem resistances could account for differences in growth rate under mild drought. Higher stem resistances will cause lower stem ψ_s and thus lower stem cell turgor pressures in meristematic zones. This in turn could cause slower growth rates in *Q robur versus Q petraea* (Cosgrove, 1986). More studies will be necessary to determine the effect of differences in shoot resistance on differences in performance of tree species during drought.

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