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Original article

Use of pressure volume curves in water relation analysis on woody shoots: influence of rehydration and comparison of four European oak species

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Summary – Pressure volume analyses were undertaken on leafy shoots of 4 European oak species (*Quercus robur, Q petraea, Q pubescens* and *Q ilex*) in order to determine the relationship between leaf water potential, average osmotic potential and volume averaged turgor. Some technical limitations of pressure volume analysis, as shown by the influence of the resaturation method on computed turgor, were overcome by accounting for losses of intercellular water during the first stages of dehydration. Variations in leaf to stem ratio, which are very important between large leaved oaks and small leaved evergreens, surprisingly did not influence the relative symplasmic volume of our samples. Differences in mean osmotic potential at full turgor (Π_0) were related to species, with higher values in drought adapted species, and to leaf age and growing conditions. Values of volumetric modulus of elasticity (ε_0) did not significantly influence the relations between leaf water potential (Ψ_w) and turgor (*P*) in different species. This relationship was mostly related to Π_0. Finally, tolerance to drought appeared to be related more to the ability to osmotically adjust in response to changes in environment rather than to the absolute values of Π_0.

water relations / *Quercus sp* / water potential / turgor / pressure-volume curve

Résumé – Utilisation de courbes pression/volume dans l'analyse des relations hydriques de rameaux feuillés: influence de la réhydratation et comparaison de quatre espèces de chênes européens. *Une analyse des relations hydriques de rameaux feuillés de 4 espèces de chêne (*Quercus robur, Q petraea, Q pubescens, Q ilex*) a été entreprise à l'aide de la technique des courbes pression-volume, afin de préciser les relations existant entre le potentiel hydrique foliaire, le potentiel osmotique moyen et la pression de turgescence moyenne. Un certain nombre de limites techniques dues par exemple, à la méthode de réhydratation des échantillons végétaux, ont été dépassées par la prise en compte des pertes*

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d'eau intercellulaire se produisant durant les premiers stades de déssèchement. Des variations importantes du rapport des biomasses feuilles/tiges, liées à la morphologie des espèces (grandes feuilles des chênes médioeuropéens par rapport aux sclérophylles des chênes verts), n'ont pas eu d'influence sur l'estimation du volume symplasmique relatif. Des différences importantes apparaissent dans les valeurs de potentiel osmotique à pleine turgescence (Π_0), en premier lieu entre espèces, avec des valeurs plus élevées pour des chênes adaptés à la sécheresse, mais aussi en fonction de l'âge des feuilles et des conditions dans lesquelles s'est efffectuée la croissance des arbres. Les valeurs prises par le module d'élasticité volumique (ε_0) n'influencent que peu les relations entre potentiel hydrique foliaire (Ψ_w) et turgescence (P), qui en fait dépendent étroitement de celle de Π_0. Enfin, les différences dans le degré de tolérance de périodes de sécheresse paraissent plus liées à la capacité des arbres à mettre en œuvre un ajustement osmotique en réponse aux perturbations de leur environnement qu'aux valeurs absolues de Π_0.

relations hydriques / Quercus sp / potentiel hydrique / turgescence / courbe pression-volume

INTRODUCTION

The genus *Quercus* contains a wide variety of species that exhibit very different ecological habits. In Europe, the most important species for forestry are *Quercus robur L* and *Q petraea* (Matt) Liebl. Both species belong to the section *robur* of the subgenus *Lepidobalanus* (Krusmann, 1978), and are mostly found in regions with few and limited periods of drought. Other species, such as *Q pubescens* Willd (subgenus *Lepidobalanus* section *robur*) and *Q ilex* (an evergreen sclerophyll, subgenus *Lepidobalanus* section *ilex*), are located on drier sites in Southern Europe.

Ecological studies conducted in oak stands have shown differences between *Q petraea* and *Q robur* in their ability to survive a severe summer drought, such as the drought of 1976 in Western Europe when the former species was observed to be more resistant than the latter (Becker and Lévy, 1982). A variety of mechanisms may be responsible for these differences; these include better soil colonization by roots, more efficient control of water loss during stress periods, and/or a better ability to tolerate leaf water deficits.

Tolerance of leaf water deficits is mainly related to elastic properties of cell walls and to osmotic water potential at full turgor (Π_0). Larger values of Π_0 imply a better maintenance of cell turgor (*P*) at a given leaf water potential (Ψ_w) (Tyree and Jarvis, 1982). A larger cell wall elasticity limits decreases in *P* with decreasing Ψ_w. Variability of Π_0 in a great range of American hardwoods has been reviewed recently by Abrams (1988b). He emphasized that variations within a given species are often larger than those between species, and that variations were related to leaf age, local stand conditions, and physiological adaptation to recurrent drought through osmo-regulation.

Water relation parameters are most often obtained by establishing so-called "pressure-volume relations" (Tyree and Hammel, 1972). However, the use of this technique with woody shoots may yield some artifacts due to the variable ratio of foliar to associated stem tissues in samples (Neufeld and Teskey, 1986), and, therefore, to the presence of larger amounts of apoplastic water in stem *versus* leaf tissues.

In this paper, we describe the water relations obtained with the pressure-volume method on leafy shoots of 4 oak species growing under a given set of environmental conditions. Before undertaking interspecific comparisons, the effects of rehydration techniques on computed water relation parameters were evaluated and these results were used to adjust values of the parameters used to develop the species comparison.

MATERIAL AND METHODS

Water potential isotherms were established using the transpiration method described by Hinckley *et al* (1980), where a shoot is transpiring freely, and its weight and water potential are recorded at regular intervals.

Theory

Theory of pressure-volume curves has been established by Tyree and Hammel (1972). Pairs of values of leaf water potential Ψ_w and leaf saturation deficit *D*, corresponding to successive states of dehydration, are plotted as:

$$1/\Psi_w = f\,(D)$$

This expression relies on the hypothesis that all changes in leaf water content are due to changes in symplasmic water content, and that the apoplastic and intercellular water content remain constant. Such a curve, as shown in figure 1, displays a linear region where turgor is equal to 0. A linear regression (least squares analysis) through the points of this straight segment results in equation (1):

$$1/\Psi_w = 1/\Pi = a\,(D) + b \approx V_{si}/N_s\,RT \quad (1)$$

where Π is the volume averaged osmotic pressure of the leaf, *a* the slope of the fitted line, *b* the *Y*-axis intercept, V_{si} the actual symplasmic volume of the leaf, N_s the total number of moles of solutes present in the vacuoles, R the gas constant and *T* the absolute temperature.

Because:

$$V_{si} = V_s - D\,(V_s + V_a)$$

where V_s is the symplasmic volume at full turgor and V_a the apoplastic volume, equation (1) may be transformed into:

$$1/\Psi_w \approx V_s/N_sRT - D\,(V_s/N_sRT + V_a/N_sRT)$$
$$\approx 1/\Pi_0 - D\,(1/\Pi_0 + V_a/N_sRT)$$

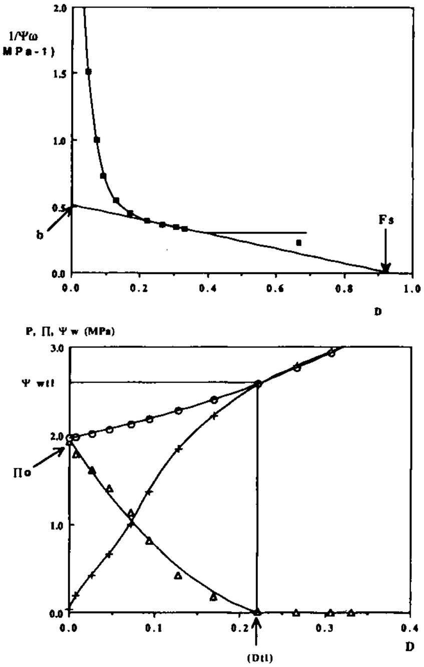


Fig 1. Example of results derived from a "pressure-volume" analysis. (*a*). Typical pressure volume curve obtained with a transpiring leafy shoot of *Q ilex*; *D*: leaf water deficit, Ψ_w: leaf water potential (MPa); the linear portion is adjusted to a straight line intercepting *Y-axis* at $b = 1/\Pi_0$, and *X-axis* at $b/a = F_s$ (see text for details). (*b*). Höfler diagram constructed from previous data, showing the evolution of osmotic potential Π (circles), leaf water potential Ψ_w (crosses) and volume averaged turgor *P* (triangles) with *D*. Initial slope of $P = f(D)$ is the volumetric modulus of elasticity ε_0 (see text for details about computation).

where Π_0 is the osmotic pressure at full turgor.

The significance of both regression coefficients in equation (1) appears clearly:

$$b = 1/\Pi_0 \text{ and } b/a = V_s\,(V_a + V_s) = F_s$$

where F_s is the symplasm fraction of the leaf. This estimation is obtained through an extrapolation of the linear regression toward the *X*-axis (fig 1). There is, however, some uncertainty regarding this value (Tyree and Richter, 1982).

The non-linear fraction of the curve is described by:

$$P = \Psi_w - \Pi$$

where Π is derived from equation (1) and *P* is the volume averaged turgor. The behaviour of *P* with changes in *D* is related to cellular elasticity. The volumetric modulus of elasticity is estimated as (Tyree and Jarvis, 1982; Fanjul and Rosher, 1984):

$$\varepsilon = V_{si}\ \mathrm{d}P/\mathrm{d}V_{si}$$

and changes in P with changes in D as:

$$\mathrm{d}P/\mathrm{d}D = -\ (V_a + V_s)\ \mathrm{d}P/\mathrm{d}V_{si}$$

and by substitution:

$$\varepsilon = V_{si}\ (V_a + V_s)\ \mathrm{d}P/\mathrm{d}D$$

which may be approximated by:

$$\varepsilon \approx RWC\ \mathrm{d}P/\mathrm{d}D$$

At full turgor, RWC is equal to 1, and volumetric modulus of elasticity at full turgor ε_0 is calculated as:

$$\varepsilon_0 \approx -\mathrm{d}P/\mathrm{d}D$$

The function $P = f(D)$ is fitted to a second order polynom $\alpha D^2 + \beta D + \chi$, and the modulus of elasticity therefore corresponds to the value of the derivated function $2\alpha D + \beta$ for $D=0$, that is β.

Plant material

Measurements were taken partly in Avignon and partly in Nancy on leafy shoots of the following species:

Quercus robur L and *Q petraea* (Matt) Liebl (measurements in Nancy). Seedlings of these 2 species originated from the Office National des Forêts nursery at Villers-lès-Nancy and were grown for 4 years in pots containing 30 l of a sandy-loam, in a greenhouse, at Champenoux (near Nancy); irrigation was manual. Both species were visually differentiated based on their leaf morphology, *Q petraea* by its differentiated petiole and *Q robur* by its well defined ears on the base of the lamina. In order to assess the effect of natural stand conditions, 30-year-old *Q petraea* trees (dominant height: about 12 m) grown in Champenoux "Forêt Domaniale" were also used. Shoots were collected on 4 different individuals by rifle shooting; only leaves exposed to full light were selected. Collection was undertaken in August-September after a period of natural water shortage.

Thirty-year-old trees of *Q pubescens* Willd and *Q ilex* L growing in natural stands near Avignon in Southern France were studied. Only well developed adult leaves were used for the measurements. However, in the case of the sempervirent species *Q ilex*, measurements were made either on previous year leaves (in April), later called "old" leaves, or on current-year leaves (in July, "young" leaves). For all species, leafy shoots, bearing 4-10 leaves, were harvested at the end of the afternoon.

Table I. Main features of experimental treatments: *L/S* is the ratio of leaf to woody biomass on tested shoots, *A* is the total leaf area of the samples and *n* is the number of replicates in each treatment. (*A*) Test of rehydration techniques (immersion *vs* stem rehydration) (B) Comparisons between species. See text for further details. Values followed by the same letter are not significantly different.

A	*Species*	*Origin*	*Sample preparation*	*L/S*	*n*
	Q ilex	Avignon	immersion	2.14 *a*	7
			12 h stem rehydration	1.40 *a*	8
			24 h stem rehydration	1.70 *a*	4

B	*Species*	*Origin*	*Sample type*	*L/S*	*A (dm²)*	*n*
	Q ilex	Avignon	old leaves (April)	1.89±0.65 *a*		38
	Q ilex	Avignon	young leaves (July)	2.73±0.67 *ab*	0.21 a	14
	Q pubescens	Avignon	July	2.90±0.48 *b*	0.53 *b*	15
	Q robur	Champenoux	May, glasshouse	5.67±0.86 *c*	1.05 *b*	19
	Q petraea	Champenoux	May, glasshouse	4.10±0.71 *c*	1.25 *c*	21
	Q petraea	Champenoux	August-September 40year old stand	3.22±0.57 *b*		32

Rehydration techniques

Three different rehydration techniques were tested on *Q ilex* shoots during April prior to extensive experiments (table I):

- standard method: the cut stem was plunged into tap water and stored at 4-10 °C, in darkness for 12 h;
- 24 h rehydration: the same technique was applied, but rehydration last for 24 h;
- immersion: the leafy shoot was completely immersed under water at 4-10 °C in darkness for 12 h.

Pressure-volume parameters

Pressure-volume relations were established as follows: water was carefully removed from a rehydrated shoot, and the shoot was then weighed to establish full turgor fresh weight (FW_{ft}). The corresponding water potential was measured with a pressure chamber, in which pressure was gradually increased (+0.3 MPa min^{-1}) until the appearence of a sap meniscus at the cut end occurred. The balance pressure was recorded with a pressure transducer Protais CPM 20 and a milli-Voltmeter. Pressure was released at the same low rate, and the shoot was allowed to transpire for about 20 min. This procedure was repeated until water potential reached values of about −4 MPa.

The absence of any significant weight loss during pressurization was verified. After reaching −4.0 MPa, leaves and stems were desiccated at 85 °C for 48 h, and weighed separately. The dry weight ratio of leaves/stem (*L/S*) was calculated, and the saturation deficit corresponding to successive dehydrations was estimated from:

$$D = 1 - (FW - DW) / (FW_{ft} - DW)$$

where *FW* is the shoot fresh weight and *DW* the dry weight.

RESULTS

Effects of rehydration technique on calculated water relation parameters (Quercus ilex, *old leaves)*

Figure 2a shows 2 pressure-volume curves, 1 obtained from a twig "normally" rehydrated (*ie*, through the stem) and the other from a twig completely immersed for 12 h. These data were used to compute the relationship between leaf saturation deficit (*D*) and measured water potential (Ψ_w) as shown in figure 2b. A considerable difference exists between the 2 curves; the first steps of dehydration for the immersed sample are not accompanied by any significant change in Ψ_w. After these initial dehydration steps, the pattern of both curves is similar, and may be described by a second order polynomial. Intersection of each curve with the Y-axis approximates the shift δ in *D* due to water losses without appreciable changes in Ψ_w. This shift is present for immersed samples alone and is absent for most stem rehydrated samples. This difference is probably due to an oversaturation of apoplasmic and intercellular spaces in leaves and stems because of immersion.

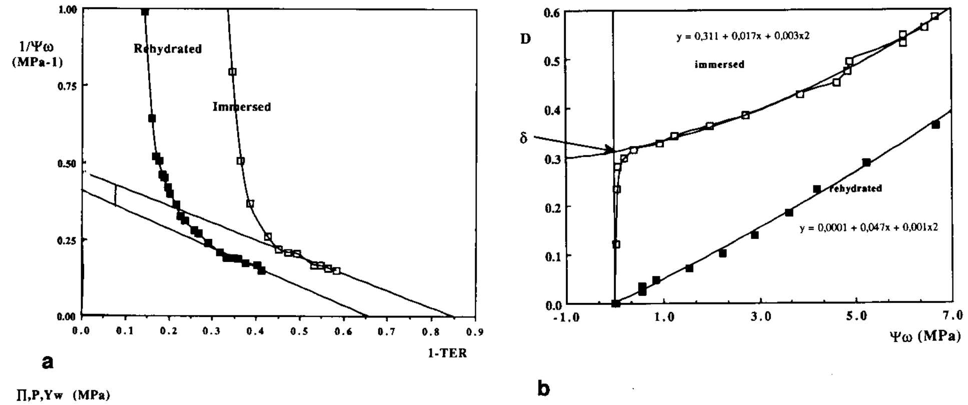
Plotting the results obtained with an immersed sample on a Höfler diagram (fig 2c) shows the spurious effects of over resaturation on calculated turgor pressure (*P*): a long plateau appears before the typical decrease in *P* with *D*. We may correct the values of *D* for the shift (δ), using the following equation:

$$D_{cor} = (D - \delta) / (1 - \delta)$$

where D_{cor} is the new value of leaf water deficit. D_{cor} will be below 0 for all points corresponding to oversaturation. These points have been eliminated from all subsequent calculations.

Recalculation of parameters using corrected values of *D* results in a modified Höfler diagram as shown in figure 2c: the plateau in *P* has completely disappeared, and *P* evolution is similar to the general model.

Statistical results shown in tables II and III confirm that these shifts (δ) appear in all pressure-volume data obtained with immersed samples. They attain a mean value of 0.3 with im-



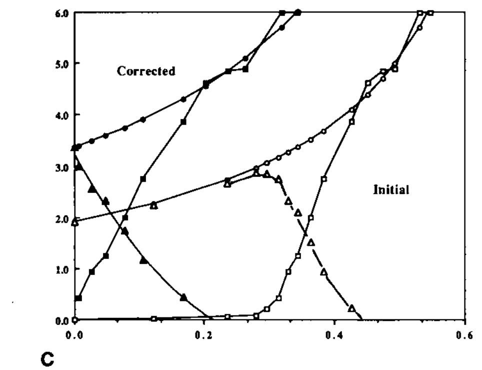


Fig 2. Effects of sample rehydration technique on results. (*a*) Pressure volume curves obtained with an immersed (open symbols) and a stem rehydrated sample of *Q ilex*. (*b*) Comparative evolution of estimated leaf water deficit *D* vs leaf water potential Ψ_w obtained from the same set of data. In the case of the immersed sample, a shift δ appears in *D*, due to water losses from the intercellular spaces. Evolution of *D* is described by a second order polynomial (equations shown) used to calculate values of δ. (*c*) The shift δ obtained in (*b*) has been used to calculate corrected values for *D*, and Höfler diagrams obtained with crude and with corrected results from the immersed sample of (*a*) are compared.

mersed samples, and values of less than 0.1 with stem rehydrated samples. Even the stem rehydration technique may result in oversaturation, but with relatively small effects on calculated *P*. Consequences of this oversaturation artifact on calculated parameters are important: Ψ_{wtl} (water potential at turgor loss) is not affected but all other parameters are. Osmotic potential at full turgor (Π_o) is underestimated while the volumetric elastic modulus at full turgor (ε_o) and the leaf saturation deficit at turgor loss (D_{tl}) are underestimated (table II).

When corrected values of *D* are used, these artifacts are minimized. Table III

Table II. Effects of correcting the calculated values of *D* by the shift observed on Ψ_w-*D* relationships (see text for details) on resulting water relation parameters; data obtained on 7 twigs of *Quercus ilex* submitted to immersion. Symbols: Π_0, osmotic potential at full turgor (MPa), ε_0, volumetric modulus of elasticity at full turgor (MPa), D_{tl}, leaf saturation deficit at turgor loss, Ψ_{wtl}, leaf water potential at turgor loss (MPa), F_s, fraction of symplasmic water. Results are compared using an Anova analysis and the Fisher PLSD test at 95%. Values followed by the same letter are not significantly different.

Treatment	Πo	εo	D_{tl}	Ψ_{wtl}	F_s	*n*
Without correction	–2.00 *a*	32.5 *a*	0.430 *a*	– 4.37 *a*	0.805 *a*	7
With correction	–3.02 *b*	19.6 *b*	0.259 *b*	– 4.32 *a*	0.714 *a*	7

Table III. Effects of the rehydration technique and corrections for apoplastic water loss on computed water relation parameters of *Quercus ilex* twigs. First line shows corrected values obtained with immersed samples. Results are compared using an Anova and the Fisher PLSD test; values followed by the same letter are not significantly different. Symbols: Π_0, osmotic potential at full turgor (MPa), ε_0, volumetric modulus of elasticity at full turgor (MPa), D_{tl}, leaf saturation deficit at turgor loss point, Ψ_{wtl}, leaf water potential at turgor loss point (MPa), F_s, fraction of symplasmic water, δ, shift in leaf water saturation deficit obtained as in figure 2.

Treatment	δ	Π_o	ε_o	*Dtl*	Ψ_{wtl}	*Fs*	*n*
Immersion (Corr)	0.27	–2.93 *a*	19.2 *a*	0.236 *a*	–4.27 *a*	0.70 *a*	13
12h rehydration	0.08	–2.50 *a*	25.6 *b*	0.247 *a*	–4.13 *a*	0.65 *a*	12
24h rehydration	0.09	–2.73 *a*	21.4 *b*	0.238 *a*	–4.05 *a*	0.66 *a*	11

shows a comparison of water relation parameters obtained with corrected values D_{cor}; no significant differences appear anymore, except for ε_o.

In the following analyses, we will use for old leaves of *Quercus ilex* mean values calculated using stem rehydration (12 or 24 h) and corrected values of *D* whenever needed.

Effects of leaf age in Quercus ilex

Results in table IV show that water relation parameters of non-current leaves of the previous year differ markedly from those of current year leaves: Π_o, Ψ_{wtl} are much lower and D_{tl} is much higher while ε_o and F_s are not affected. Therefore both groups will be con-

Table IV. Global comparison of tested species. Symbols: Π_0, osmotic potential at full turgor (MPa), δ_0, volumetric modulus of elasticity at full turgor (MPa), D_{tl}, leaf saturation deficit at turgor loss, Ψ_{wtl}, leaf water potential at turgor loss (MPa), F_s, fraction of symplasmic water, *L/S* leaf to shoot dry weight ratio. An Anova analysis and a Fisher PLSD test at 95% revealed significant differences where different letters follow shown values.

Species	Π_o *(MPa)*	δ_o *(MPa)*	D_{tl}	Ψ_{wtl} *(MPa)*	*Fs*	*L/S*
Q robur (greenhouse)	*–1.46 (a)*	16.1 (a)	0.141 (a)	–2.24 (a)	0.49 (a)	4.104 (a)
Q petraea (greenhouse)	*–1.45 (a)*	14.9 (a)	0.149 (a)	–2.04 (a)	0.53 (a)	5.648 (b)
Q petraea (adult stand)	*–2.26 (b)*	19.8 (b)	0.208 (b)	–3.04 (b)	0.83 (b)	3.218 (c)
Q pubescens (adult stand)	*–2.14 (b)*	25.5 (c)	0.186 (bd)	–2.81 (bd)	0.78 (b)	2.900 (c)
Q ilex (old leaves)	*–2.74 (c)*	21.5 (bc)	0.238 (c)	–4.14 (c)	0.68 (c)	1.893 (cd)
Q ilex (young leaves)	*–1.82 (d)*	26.6 (c)	0.156 (ad)	–2.39 (ad)	0.66 (c)	2.726 (c)

sidered separately for the general inter-species analysis.

Comparison between species and growth conditions

There are many differences between the study species (table IV). Major results will be noted briefly.

- Π_0 is highest for *Q robur* and *Q petraea* grown under a greenhouse environment. It is significantly lower in *Q petraea* and *Q pubescens* growing in stands; and the latter values appear intermediate between those of curvent and previous year leaves of *Q ilex*. The lowest value of Π_0 is observed on old foliage of *Q ilex*;
- the same ranking is noted for Ψ_{wtl} and D_{tl}; however, differences between species for these parameters, although still significant, were smaller because of increased variability;
- differences in ε_0 are not consistently significant; ε_0 seems to be lower for *Q robur* and *Q petraea* grown under a greenhouse environment;
- most striking are the results concerning relative symplasmic volume (F_S). First, the greatest values of F_S are noted in Southern, small-leaved oaks; second, the expected relationship between F_S and the leaf/stem dry weight ratio (*L/S*) does not occur; third, the species with lowest *L/S* also display the largest values of F_S. Finally, no statistical correlation was noted between F_S and *L/S* values of individual twigs for a given species-treatment (r^2= 0.11).

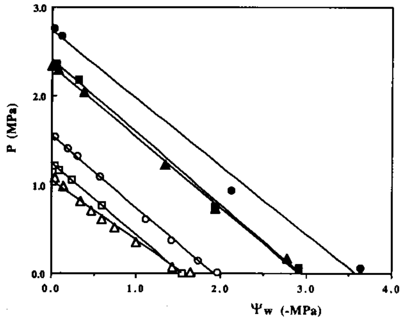


Fig 3. Relationship between turgor (*P*) and water potential (Ψ_w) for 6 sample shoots of *Q pubescens* (closed symbols) and *Q petraea* (open symbols). Curves are fitted to straight lines (r^2 better than 0.99).

Figure 3 illustrates the relations between *P* and Ψ_w obtained with 3 different *Q pubescens* and *Q petraea* individuals. These relationships are approximated by linear regressions ($r^2 \geq 0.99$). This representation shows clearly that, for a given Ψ_w, *P* is much greater in *Q pubescens* than in *Q petraea*. For *Q petraea*, this difference is mainly the result of a lower Π_0. Mean tissue elasticity does not significantly affect the relationship.

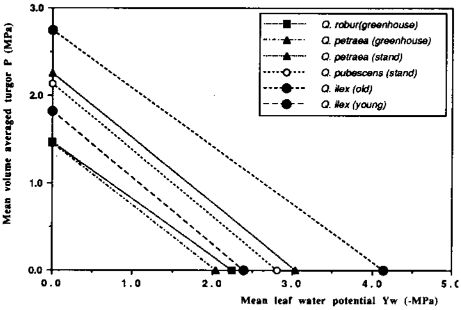


Fig 4. Summary of water relation data for tested species. Mean values of osmotic potential Π_0 for each species are recorded on *Y*-axis, and mean leaf water potential at turgor loss (Ψ_{wtl}) on *X*-axis. The straight line between both closely approximates a mean *P* -Ψ_w relationship for each species, indicating the ability of a species leafy tissue to maintain *P* when submitted to decreasing Ψ_w. Clear differences appear between species. Standard errors are not presented for the sake of clarity.

We used the fact that the *P*/Ψ_w relationship is nearly linear to present our results in a synthesis diagram: mean values of Π_0 for each species, which are equal to the mean maximal *P*, are connected by a straight line to the mean values of Ψ_{wtl}. This line approximates the mean relationship between P and Ψ_w for all species (fig 4). Differences between groups are largely due to variations in the estimate pressure-volume parameters.

DISCUSSION

Pressure volume relations on leafy shoots from woody species

Possible artifacts arising from the use of the pressure-volume technique to estimate water relation parameters for woody twigs have been frequently discussed (Neufeld and Teskey, 1986; Turner, 1988). The choice of the free transpiration *versus* the within chamber pressurization method is not clear as discrepancies with both methods have been noted (Ritchie and Roden, 1985; Parker and Pallardy 1988a; Hardegree, 1989). These discrepancies were mostly minor and both methods are now generally accepted.

One criticism of the free transpiration method is the fact that intercellular water content in leaves may change during measurement. In fact, we have demonstrated that such changes occur, and that they depend largely on the technique used for sample rehydration. During the first steps of dehydration, apparent leaf water deficit (D) increases without a parallel decrease in water potential (Ψ_w). These findings confirm those of Ritchie and Shula (1984) and Parker and Pallardy (1987). Such behavior was attributed by Turner (1988) to membrane damage caused by the high turgor pressure in cells. In the case of xeric plants displaying very low Ψ_w, rehydration is also accompanied by solute transfers causing changes in Π_0 (Evans *et al*, 1990). In our case, the observed effects appeared most frequently with immersed shoots, and only occasionally with normal stem rehydrated shoots. As suggested by others (*eg*, Parker and Pallardy, 1987), these results indicate that the changes in D without a change in Ψ_w are due to an oversaturation of intercellular volumes in leaves and stems during rehydration, and that this water is lost during the first steps of dehydration.

This artifact stongly affects the relationship between P and D, resulting in a "plateau" before decreasing normally with increasing D. Such plateaus have been directly or indirectly described by other investigators (Kandiko *et al*, 1980; Parker *et al*, 1982; Dreyer, 1984; Ritchie and Shula, 1984; Guyon, 1987), but have never been convincingly explained. Correcting the values of D for the oversaturation with our method yields results of the same magnitude as those obtained with standard methods, exhibiting an immediate decrease of P with increasing D.

It should be noted that light oversaturation effects also occur with standard stem rehydration; we may therefore conclude, as did Turner (1988), that short rehydration periods of a few hours should be used when possible. In addition, Meinzer *et al* (1986) have demonstrated that resaturation may eliminate any transitory diurnal osmotic adjustment.

Varying leaf/stem ratio (L/S), for example with smallleaved shoots of *Q ilex vs* large leaved shoots of *Q petraea* or *Q robur*, could possibly modify some estimated parameters, because the ratio of symplasmic to total water volume (F_s) probably varies. However, Neufeld and Teskey (1986) examined the effects of defoliating twigs (*ie* modifying L/S); Π_0 and Ψ_{wtl} estimates did not change significantly. They also obtained a curious result: their defoliations did not promote a reduction in the estimate of the relative symplasmic volume F_S. In our study no significant correlation was detected between individual values of *L/S* and F_S. The effect of varying stem volumes on F_S estimates remains a major problem of pressure-volume analyses on woody shoots.

Effects of leaf age

A comparison between 2 age classes of *Q ilex* leaves (current year leaves in July and previous year leaves in April) confirms previous results regarding the effects of leaf age: both Π_0 and Ψ_{wtl} decreased (Roberts *et al*, 1980; Doi *et al*, 1986), and the volumetric modulus of elasticity ε_0 remained relatively constant (Roberts *et al*, 1980; Parker *et al*, 1982). It is not clear whether these effects are due to leaf ageing alone, or to drought preconditioning during the previous summer.

Comparing oak species

Our results allow a clear separation of studied species into 2 groups. The 1st group is composed of both mesic species from Northern France, *Q robur* and *Q petraea*, cultivated under a greenhouse environment with optimal watering. The 2nd group is composed of *Q petraea* under stand conditions and the more xeric species from Southern France (*Q pubescens* and *Q ilex*). The 1st group showed very similar results, while greater variability appeared in the 2nd.

The most striking result is the large difference between young trees growing in a greenhouse and older trees growing in a stand as shown by results from *Q petraea*. The difference between greenhouse saplings and mature trees was 0.8 MPa for Π_0 and 1.0 MPa for Ψ_{wtl}. These very large differences may be due to acclimation to the summer drought experienced by the stand during the year of measurement. Active adjustment of Π_0 in response to drought has been reported for various tree species, but adjustments are typically less than 0.5 MPa. The following values have been reported for a wide set of species: 0.50, 0.54 and 0.26 MPa for *Quercus alba*, *Q macrocarpa* and *Q stellata* respectively (Parker and Pallardy, 1988b), 0.60, 0.23 and 0.13 MPa for *Q acutissima*, *Q alba* and *Q stellata* (Ki and Pallardy, 1989), 0.4 MPa in *Tsuga heterophylla* (Kandiko *et al*, 1980), 0.3 to 0.4 in *Malus domestica* (Fanjul and Rosher, 1984), 0.3 to 0.4 in *Eucalyptus microcarpa* (Myers and Neales, 1986) and 0.2 in *Rosa hybrida* (Auge *et al*, 1986). In our case, a simple osmotic adjustment may not account fully for the large differences between greenhouse saplings and mature trees. Light regime and possibly mineral nutrition may also have a strong effect on water relation parameters. These results indicate that further data concerning drought preconditioning are needed for oak seedlings; such data would be very important in understanding the production of drought hardened seedlings for transplanting.

These large differences in Π_0, which appeared in response to changing environmental conditions (greenhouse *versus* stand), reveal an important plasticity among species; it is therefore very risky to compare tree species on the basis of published data on Π_0 and other water relation parameters. Nevertheless, a quick glance at Π_0 and Ψ_{wtl} values in different oak species (table V) allows a schematic ranking of species. Values for our greenhouse trees appear high as compared to those of most other oak species; only *Q ellipsoidalis* showed higher values. Other mesic species have a similar range of values, *eg*, *Juglans nigra* (–1.47 and –2.04 MPa, Parker and Pallardy, 1985), *Juglans regia* (–1.3 and

Table V. Mean values of osmotic potential at full turgor (Π_0, MPa) and of water potential at turgor loss (Ψ_{wpt}. MPa) measured on different species in the genus *Quercus*. Available information on growth conditions is presented (dry: following a period of natural drought, greenh: grown under greenhouse conditions; trees are growing under stand conditions if not specified).

Species	*Section*	Π_0	Ψ_{wpt}		*Reference*
Quercus ilex	*ilex*	−1.82	−2.39	(young)	this paper
		−2.43	−4.10	(old)	this paper
Quercus pubescens	*robur*	−2.5±0.4	−4.0±0.5		Guyon, 1987
		−2.14	−2.81		this paper
Quercus rubra	*rubrae*	−2.0±0.1	−2.5±0.2		Dreyer, unpublished
		−1.76	−2.62		Parker *et al*, 1982
		−1.98	−2.67		Bahari *et al*, 1985
Quercus velutina	*rubrae*	−2.26	−2.73		Baheri *et al*, 1985
Quercus petraea	*robur*	−2.26	−3.04		this paper
		−1.45	−2.04	greenh	this paper
Quercus muehlenbergii	*albae*	−2.05	−2.61		Abrams and Knapp, 1986
Quercus macrocarpa	*albae*	−1.56	−2.04		Parker and Pallardy, 1988b
		−2.10	−2.66	dry	Parker and Pallardy, 1988b
		−2.40	−3.02		Abrams and Knapp, 1986
Quercus stellata	*albae*	−1.82	−2.48		Abrams and Knapp, 1986
		−2.08	−2.81	dry	Parker and Pallardy, 1988b
Quercus alba	*albae*	−1.67	−1.99		Parker and Pallardy, 1987
		−1.97	−2.64		Parker *et al*, 1982
		−1.47	−2.02		Parker and Pallardy, 1988b
		−1.95	−2.53	dry	Parker and Pallardy, 1988b
Quercus robur	*robur*	−1.46	−2.24	greenh	this paper
Quercus ellipsoidalis	*rubrae*	−0.83	−0.99	May	Abrams, 1988a
		−1.2	−1.72	July	Abrams, 1988a

−1.9 MPa, Dreyer, 1984), *Acer saccharinum* (−1.4 and −2.3 MPa, Cheung *et al*, 1975). Stand grown trees of *Q petraea* and the 2 mediterranean species have much lower values of Π_0 and Ψ_{wtl} than those of most species. Similar low values have been observed in *Malus domestica* (−2.2 and −3.3 MPa, Fanjul and Rosher, 1984) and *Olea oleaster* (−2.0 and −2.9 MPa, Lo Gullo and Salleo, 1988).

Significant differences appear between species in the volumetric modulus of elasticity (ε_0). Its values are lower (higher elasticity) in *Q robur* and *Q petraea* than in *Q pubescens* and *Q ilex*, due to the greater sclerophylly of Southern oaks. The leaf saturation deficit at turgor loss (D_{tl}) is also higher in the Southern oaks.

It is generally accepted that the best criterion for desiccation tolerance is the ability to maintain a high turgor *P* when transpiration or soil water conditions impose a low leaf water potential Ψ_w (Turner, 1988). Relationships between mean values of *P* and Ψ_w show clear differences between species in this regard. The degree of desiccation tolerance is rather obvious: *Q ilex's* older leaves are the most tolerant, followed by *Q pubescens* and *Q petraea* in stands then *Q ilex* young leaves, and finally by *Q petrae* and *Q robur* grown in a greenhouse.

What can be the role of observed differences in Π_0 and Ψ_{wtl} in the ability of tree species to tolerate dry environments? These differences may be less important than generally suggested. In fact, the large plasticy observed with the species *Q petraea* suggests a major role of environmental conditions in promoting adjustments to drought. Furthermore, the fact that *Q petraea* in stands at Nancy and *Q pubescens* at Avignon have about the same Π_0 and Ψ_{wtl} values indicates that these parameters only play a minor role in drought tolerance. As also stated by Lo Gullo and Salleo (1988) with sclerophyllous plants, osmotic potential *per se* may not be an index of drought tolerance. Other physiological parameters should be tested, such as the stability of water conduction under drought, or even interactions between water and carbon budgets. These conclusions need to be confirmed in further studies on oak stress physiology, in which the plasticity of water relations and hydraulic functions should be examined in parallel.

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