Original article

Field comparison of transpiration, stomatal conductance and vulnerability to cavitation of *Quercus petraea* and *Quercus robur* under water stress

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Summary — Water relations were analysed in adult oaks (*Quercus petraea* and *Q robur*) during a period of water shortage in a simplified lysimeter. Sap flux densities and stomatal conductance were reduced by ≈ 70% at maximal drought intensity. Predawn leaf water potential then ranged from –1.7 to –2.0 MPa. The slightly lower transpiration observed in pedunculate oaks could be ascribed to their smaller crown development. Nevertheless, no significant difference in stomatal conductance could be observed between the two species. They also had the same percent loss of conductivity (≈ 80%) in petioles at maximal drought intensity when midday leaf water potential had dropped to ≈ –3.0 MPa. Finally, good agreement was found between observed losses of hydraulic conductivity during *in situ* dehydration and the vulnerability curves obtained under laboratory conditions. The shifts in maximal conductivity observed in some droughted trees probably accentuated discrepancies between field and laboratory data. However, a correction procedure helped overcome these artifacts.

drought / xylem / cavitation / stomatal conductance / sap flux / *Quercus petraea* / *Quercus robur*

Résumé — Comparaison en conditions naturelles de la transpiration, de la conductance stomatique et de la vulnérabilité à la cavitation de *Quercus robur* et *Q petraea* soumis à un stress hydrique en forêt de Champenoux (France). *L'étude compare le comportement hydrique de chênes sessiles (Quercus petraea) et pédonculés (Q robur) adultes en conditions de dessèche- ment du sol. Les mesures de flux de sève et de conductance stomatique ont montré une diminution de 65 à 70% de ces paramètres au maximum de la sécheresse. Les potentiels de base atteints*

étaient alors compris entre −1,7 et −2,0 MPa. Une transpiration légèrement plus faible observée pour le chêne pédonculé a été interprétée comme résultant de différences dans le statut social des 2 espèces. Toutefois, aucune différence significative de conductance stomatique n'a pu être mise en évidence entre les 2 espèces, qui apparaissent toutes 2 comme assez tolérantes à la sécheresse. Au plus fort de la sécheresse, les 2 espèces ont montré des pourcentages d'embolie de l'ordre de 70 à 80% dans leurs pétioles, alors que le potentiel hydrique foliaire minimum atteignait −3,0 MPa. Enfin, une bonne concordance entre les mesures de perte de conductivité réalisées lors du dessèchement in situ, *et les courbes de vulnérabilité établies au laboratoire a été mise en évidence. Cependant, des dérives de conductance maximale en cours de sécheresse ont été à l'origine de certaines des différences observées. Dans ce cas, une procédure de correction du pourcentage d'embolie a permis de contrebalancer cet effet.*

chêne sessile / chêne pédonculé / flux de sève / cavitation / sécheresse / conductance stomatique / xylème

INTRODUCTION

The distribution of species in the genus Quercus (oaks) depends partly on water availability. Large differences in drought tolerance are found among oak species. Among western European oak species, sessile oak *(Quercus petraea)* is known to be more tolerant to water shortage and to require less fertile soils than pedunculate oak *(Quercus robur)* (Becker *et al,* 1982).

In the northern half of France, deep soils with high fertility and periods of waterlogging, due to the presence of a clay layer, are common (Pardé, 1942). On these sites, sessile and pedunculate oaks can grow together. They are found in mixed stands comprised of small groups of each species rather than being intermixed. Becker (1986) showed differences in vigor and growth rates between species, with sessile having a clear advantage over pedunculate oak. This observation is also confirmed by forest managers. When both *Q robur* and *Q petraea* grow together in the same site, sessile oak is always taller, larger in diameter and healthier than pedunculate oak. Some forest management texts even suggest replacing the latter by the former whenever possible (Poskin, 1934).

Furthermore, periods of oak decline and dieback occurred following the 1976 drought. The drought affected mainly pedunculate oaks (Becker and Lévy, 1982). Apparently, this species appears to be more sensitive to dry periods. On the other hand, we concluded recently (Bréda *et al,* 1993) that sessile oak was rather drought-tolerant, as are most North American oaks (Abrams, 1990).

An explanation for these frequently observed differences in the ecological requirements of both species may be related to water transport efficiency, and to possible involvement of cavitation and embolism in stress reactions. Cochard *et al* (1992) showed that *Q robur* was more prone to water-stress-induced embolism than *Q petraea.* However our measurements were made on branches rapidly dehydrated under laboratory conditions. These observations have to be confirmed with adult trees under natural conditions, and the importance of cavitation in drought reactions of trees in the stand has to be assessed (Cochard *et al,* 1992).

This paper presents a comparative analysis of water relations between trees of these 2 species growing in a natural mixed stand. Sensitivity of mature trees to drought was assessed using an imposed water shortage in a simplified lysimeter.

Seasonal time-course of water relations of both watered and droughted trees was monitored and analysed.

MATERIAL AND METHODS

Experimental plots

Effects of water stress on Q petraea and Q robur were compared in 2 groups of 8 trees (4 of each species) in a 30-yr old, 16-m high mixed stand in the Forest of Champenoux, near Nancy, France (48°44N, 6°14E, elevation: 237 m). Two scaffolding towers allowed measurements in the crowns, each giving access to 4 trees of each species. These experimental plots have been extensively described elsewhere (Bréda et al, 1993) and consist of a control plot and a dry plot. The dry plot consists of a 5 x 5 m square that includes 17 trees and is surrounded by a 1.4-m deep trench. A water-tight roof covered the soil below the crowns. The comparative study was carried out during 2 successive seasons:

– During 1991, the control plots was left under natural conditions during the first part of the season and watered by manual irrigation at the end of August (d 241, 2 irrigations of 60 mm each). In the dry plot, water supply was withheld since end of June (day 170). Unfortunately, a late frost in spring immediately after leaf emergence completely killed the bursting buds and induced a 3-wk delay in leaf flushing. A limited rehydration occurred in this treatment as a consequence of leaks which occurred during a thunderstorm (d 278, Oct 4). The whole lysimeter was completely rewatered in late autum, after all the leaves had fallen (d 317, Nov 13), by manually adding 90 mm water and removing the roof.

– During winter 1991–1992, natural rainfall completely resaturated the soil.

– During 1992, the control plot was kept well watered by natural and manual irrigation during the measurement period. The lysimeter was covered before bud-break (d 60, end of February). The rewatering occurred on October 8 (d 282), before litter-fall, by applying 150 mm water.

The number of trees studied in each plot has been presented in table I.

Table I. Number of trees measured for both species (*Quercus petraea* and *Quercus robur*) in each treatment during 1991 and 1992 experiments for potentials, stomatal conductance and sap flux density measurements.

	Control		Dry	
	Q petraea	Q robur	Q petraea	Q robur
1991	2	2	3	3
1992	1	1	2	2

Measurements

Leaf water potential was measured weekly on 2 leaves of each study tree using a pressure chamber. Leaves were sampled in the upper third of the crown just prior to dawn (predawn leaf water potential, ψ_{wp}) and at 1 pm solar time during sunny days (midday leaf water potential, ψ_{wm}). Predawn leaf water potential (ψ_{wp}) was used as an index of mean soil water in the root zone.

Sap flow was monitored on all study trees using a continuously heated radial flowmeter all over the growing season (Granier, 1985, 1987). This device allows measurement of sap flux density (Fd, $dm^3 \cdot dm^{-2} \cdot h^{-1}$) along a radial axis (2 cm long) in the xylem. Total sap flux ($dm^3 \cdot h^{-1}$) was calculated by multiplying sap flux density (F_d) by the sapwood cross-section at the same height in the trunk. Stand transpiration was computed from sap flow measurements by taking into account the statistical weight of the sampled trees in the stand. This experimental procedure has been described by Bréda et al (1993).

Midday stomatal conductance of water vapor g_s was measured between 11 and 12 am solar time each week with a Li-Cor 1600 porometer (Lincoln, NE, USA) on 5 to 10 sun-exposed leaves on different branches from the upper half of the crown.

Soil water content was measured weekly in 8 (3 in the control plot and 5 in the dry one) 1.6-m long deep aluminium access tubes via a neutron probe (NEA, Denmark).

Assessment of embolism for the 2 oak species was made on excised petioles. Two or 3 2-yr-old branches were cut from the upper canopy of each study tree during the early morning and brought into the laboratory. All measurements were performed within 4 h on 5 to 8 petioles recut under water (Cochard *et al,* 1992). Hydraulic conductivity was measured on 2-cm long samples using the technique described by Sperry *et al* (1988) and Cochard and Tyree (1990). Acidified and de-aerated water was forced through the samples at a low pressure (7 kPa), the flow measured with a balance, and the initial conductivity (K_i) calculated from the flow/pressure ratio. Two successive periods of overpressure flushing (0.1 MPa, over a 20-min period) allowed the embolized vessels to refill. The resulting conductivity (maximal conductivity) was calculated as previously described. The ratio between initial (K_i) and maximal conductivity (K_{max}) yields the loss of conductivity according to:

$$\% \text{ loss of conductivity} = 1 - (K_i/K_{max})$$

RESULTS

Time-course of leaf water potential

Figure 1 shows the seasonal time-course of predawn and midday leaf water potentials (ψ_{wp} and ψ_{wm}) for each treatment and species during the 2 study seasons. During the first part of 1991 (fig 1a), and until the irrigation of the control plot (d 241), there was no significant difference between species in the control plot, neither for predawn nor for midday leaf water potentials. ψ_{wp} of control trees showed a strong decline from –0.5 to –1.3 MPa between the first part of the season until the end of August (d 240). In fact, control trees were water-stressed for a month till the rewatering on d 240.
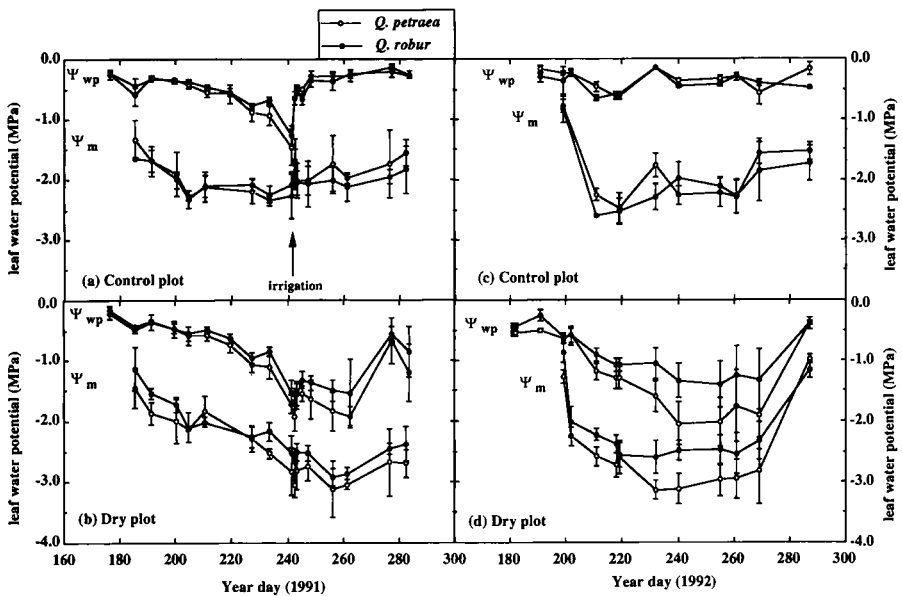

Fig 1. Seasonal time-course of predawn (ψ_{wp}) and midday (ψ_m) leaf water potential of control (a: 1991, c: 1992) and droughted trees (b: 1991, d: 1992) of *Quercus petraea* (open symbols) and *Q robur* (filled symbols). Each point represents the mean value (± SD) for 4 leaves from 2 dominant trees in the control plot, and 6 leaves from 3 dominant trees in the dry plot. Irrigation in the control plot occurred on d 241-1991 (August 29).

In the dry plot (fig 1b), ψ_{wm} was initially slightly higher in pedunculate oak than in sessile oak (d 180–210). The difference between ψ_{wp} and ψ_{wm} ($\Delta\psi_w$) increased more gradually in the former than in the latter species. This was related to the delay in leaf area index development in the former species, due to a higher sensitivity to spring-frost. Later on, drought induced a gradual and parallel decline in ψ_{wp} and ψ_{wm} until September 20 (d 263). On September 23 (d 266), a thunderstorm promoted a non-controlled and deep rewatering leading to an increase of leaf water potential. During the greatest periods of stress, values of ψ_{wp} and ψ_{wm} were slightly but consistently lower in sessile than in pedunculate oaks. A similar seasonal variation was observed during 1992, except that, as control trees were kept well watered, ψ_{wp} never dropped below −0.60 MPa (fig 1c). During 1992, the difference between sessile and pedunculate droughted trees were greater and significant for ψ_{wp} and ψ_{wm} (fig 1d).

Effects of restricted water supply on sap flux density

The daily time-course of sap flux density (F_d) in droughted trees did not display interspecific difference at the beginning of the drought period (d 210, July 29 1991; 3 trees per species, fig 2). These values were not significantly different from the mean of control trees. Nevertheless, the 2 smallest trees (one of each species) showed a lower F_d that was already observed on other suppressed trees (Bréda et al, 1993). On d 262 (September 19), drought induced a strong decline in F_d for both species. This decline appeared to be greater for the pedunculate oaks, despite their slightly higher predawn leaf water potential (ψ_{wp} = −1.54 MPa), compared to sessile oaks (ψ_{wp} = −1.75 MPa). Drought
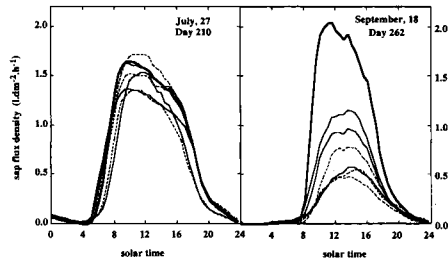

Fig 2. Diurnal time-course of individual xylem sap flux density measured on 3 droughted trees of Q petraea (line) and Q robur (dotted line) and mean sap flux calculated on 4 control trees (mean value for both species) (bold line) for 2 stress intensities: D 210: ψ_{wp} = −0.5 MPa for both treatments; D 262: control plot: ψ_{wp} = −0.3 MPa; dry plot: ψ_{wp} = −1.7 Mpa.

increased the variability in F_d within each species. Again, F_d was lower in the 2 smallest trees.

Seasonal variations of the mean daily sap flow of the 3 dry pedunculate and 3 dry sessile oaks, averaged over 10-d periods, have been shown in figure 3. A strong drought-related decrease in total transpiration occurred in both species, as compared
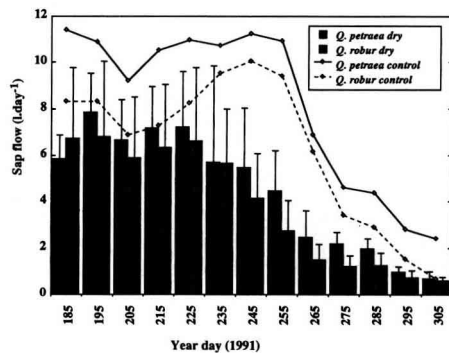

Fig 3. Seasonal time-course of the mean daily sap flow averaged over a 10-d period ($l \cdot d^{-1}$) for Q petraea (black) and Q robur (gray) in the dry and control treatments. Vertical bars indicate SD.

with control trees. During stress, sessile oaks maintained slightly higher sap flows than pedunculate oaks. This difference, even if not always statistically significant because of high within-tree variability, was nevertheless maintained during the whole period. Variations in soil water content were computed during the 2 seasons. The maximum extracted water in the lysimeter was 141 mm during 1991 and 148 mm during 1992. Soil water depletion as detected in the vicinity of root systems of both species to a 1.60-m depth was rather similar (data not shown). Nevertheless, water content profiles at the end of the dry period showed that extraction had occurred in even deeper soil layers near sessile oak roots.

Stomatal conductance

Seasonal time-course of midday stomatal conductance g_s (fig 4) displayed large vari-ations during 1991 and 1992. No difference appeared at the beginning of the 2 seasons between dry and control plots and between each species. g_s increased gradually in both species with a large variability between leaves. This may be ascribed to leaf maturation. Maximal values were ≈ 0.6 cm·s^{-1} for both species during 1991 (fig 4a,b) and somewhat higher during 1992 (0.8 cm·s^{-1}, fig 4c,d). Higher maximal values of g_s measured in 1992 may be ascribed to the better irrigation of the control plot during this year. A strong decline in g_s was observed in the control trees (fig 4a,b), which was reversed after rewatering by irrigation (d 240) and was followed by a relative stability during late summer.

In contrast, trees in the stressed plot during 1991 showed much lower values after d 240. g_s stabilised around minimal values of 0.05 cm·s^{-1} until accidental and partial rewatering (d 268) occurred. It increased slightly later on. This increase
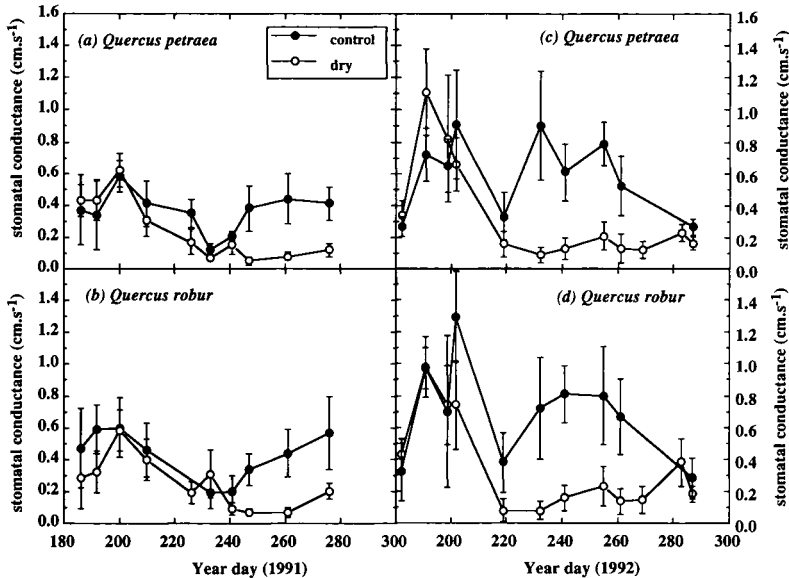

Fig 4. Seasonal time-course of mean midday stomatal conductance (± SD) measured on 10 sun-exposed leaves of the upper canopy of control (black symbols) and droughted (open symbols) trees of Q petraea (a: 1991, c: 1992) and Q robur (b: 1991, d: 1992). Control trees were irrigated on d 241, 1991.

was larger in *Q robur*. During 1992, minimal values were of the same magnitude (< 0.1 cm·s^{-1}) but were reached earlier d 220) for *Q robur* and *Q petraea* (fig 4c,d).

A general plot of g_s (values of 1991 and 1992) as a function of ψ_{wp} is presented in figure 5. For a statistical analysis of interspecific differences, data were separated into 2 classes according to their value of ψ_{wp} (below and above −0.6 MPa). Differences between species were tested (*t*-test) within each class. Neither mean values nor regressions (linear model for g_s) were significantly different between species. A sharp decrease associated with a large dispersion for predawn leaf water potential values ranging between −0.25 and −0.6 MPa was observed. Between −0.6 and −2.0 MPa the decrease in g_s was more gradual. Under most severe water stress conditions, stomatal conductance still remained at significant and constant levels of about 0.10 cm·s^{-1}, thereby allowing significant rates of leaf transpiration to continue.

Development of embolism in the field

Figure 6 shows an example of the seasonal progession of embolism on petioles of one dominant tree of each species. A significant reduction in conductivity was observed in petioles after the first measurement performed in late spring 1991, when drought had not yet begun. During 1991 (fig 6a), embolism increased after the date when ψ_{wp} was −1.8 MPa for both trees, at which time ψ_{wm} was −3.3 MPa for *Q petraea* and −2.6 MPa for *Q robur*. At this time, loss of conductivity reached 40% for *Q petraea* and 10% for *Q robur*. During 1992 (fig 6b), embolism reached 80% for *Q petraea* and 30% for *Q robur* at maximum stress intensity. The same minimal values of ψ_{wm} were observed during 1992 as well as during 1991 (−3.3 and −2.6 MPa
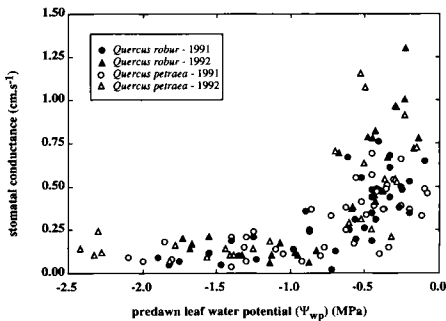
Fig 5. Midday stomatal conductance (g_s for *Q robur* (black symbols) and *Q petraea* (open symbols) plotted against predawn leaf water potential (ψ_{wp}). Data for years 1991 (circles) and 1992 (triangles) were pooled for each species. Each value is a mean of 10 replicates. Means of gs for *Q robur* and *Q petraea* were 0.56 and 0.50 cm·s^{-1} (NS) above ψ_{wp} = −0.6 MPa, and 0.19 and 0.17 cm·s^{-1} (NS) below this threshold, respectively.
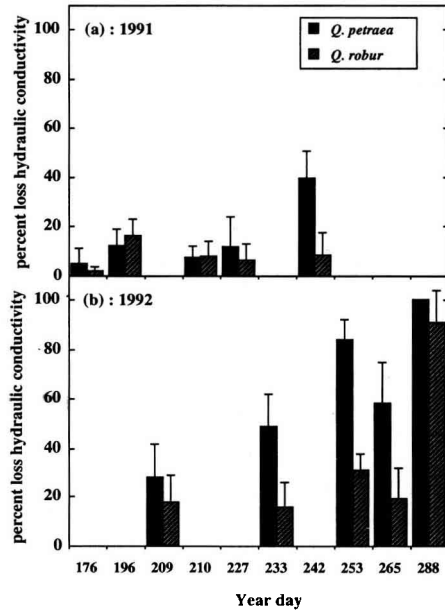
Fig 6. Seasonal progression of xylem embolism in petioles of both sessile (black) and pedunculate oaks (grey) in the droughted plot: (a): 1991; (b): 1992. Mean values of 5 to 8 replicates for 1 dominant trees of each species ± SE.

respectively for both species). We attribute
the 100% loss of conductivity that oc-
curred on d 286 in 1992 to the first frost
event (−2°C).

In situ *observed embolism*
as compared to vulnerability curves

We plotted losses of hydraulic conductivity
observed *in situ* during 1991 and 1992 on
petioles against the minimum value of mid-
day leaf water potential recorded prior to
each estimate of embolism (fig 7). The re-
sulting plot was compared with vulnerabili-
ty curves obtained on excised branches
dehydrating under laboratory conditions
(Cochard *et al,* 1992). Despite a higher
variability for *in situ* dehydration, we ob-
served good agreement between both sets
of results in sessile oak (fig 7a). However,
in the case of pedunculate oak (fig 7b), the
losses of conductivity measured on peti-
oles *in situ* seemed to remain below the
vulnerability curve between −2.5 and −3.0
MPa. But at the same time, during 1992
we observed a large decrease in the maxi-
mal hydraulic conductivity K_{max} for pedun-
culate oak in the dry plot from d 233 (Au-
gust 20) on: K_{max} decreased from 6.6 x
10^{-7} (± 5.3 x 10^{-7}) to 3.5 x 10^{-7} (± 3.3 x
10^{-7}) kg•m•s^{-1}•MPa^{-1} (in 1991, K_{max} dis-
played a mean value of 6.1 x 10^{-7} ± 2.9 x
10^{-7}). Such a decrease was not observed
in sessile oak, where K_{max} remained con-
stant during the entire season (11 x 10^{-7} ±
2.6 x 10^{-7} kg•m•s^{-1}•MPa^{-1}). The tech-
nique used to restore maximal conductivity
in the petioles did not fully resaturate the
embolized vessels during late summer and
led to a value of K_{max} which was signifi-
cantly lower than the pre-stress maximal
conductivity. We recalculated the percent-
age of embolism using the average values
of K_{max} measured before the decrease be-
gan. As shown in figure 8, corrected val-
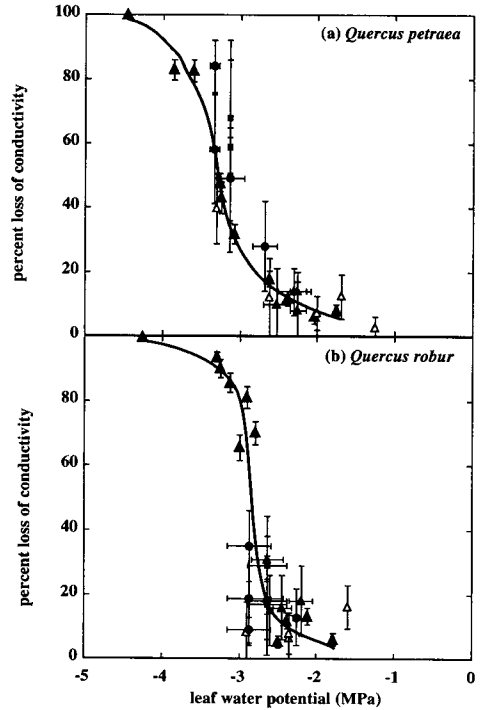ues of losses of hydraulic conductivity

Fig 7. Comparison between vulnerability curves
(large triangles) to cavitation for petioles of *Q
petraea* (a) and *Q robur* (b) (data from Cochard
et al, 1992) and losses of conductivity observed
during *in situ* dehydration. Each symbol repre-
sents a different tree, open symbols are for the
1991 measurements. Bars are SD calculated on
5 to 8 replicates for hydraulic conductivity and 3
replicates for water potential.

agreed well with the vulnerability curve ob-
tained in the laboratory.

DISCUSSION AND CONCLUSION

Although oak transpiration was reduced
under drying soil conditions, it remained
quite high even for $\psi_{wp} \leq -1.7$ MPa: it was
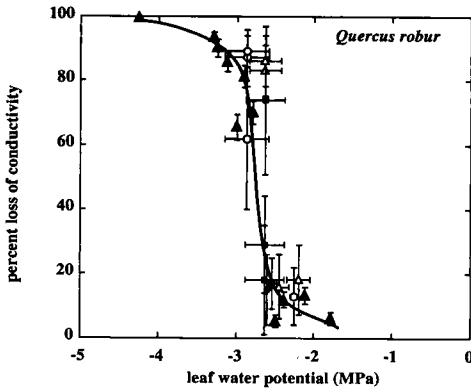reduced by ≈ 75% when water stress was

Fig 8. Comparison of corrected values of hydraulic conductivity losses with the vulnerability curve (large triangles) established under laboratory conditions on petioles of *Q robur*; corrected values (open symbols) are calculated by using the pre-stress value of maximal hydraulic conductivity throughout the season.

maximum. We have shown in a recent paper (Bréda *et al*, 1993) that sessile oak was characterized by an efficient and deep root system. We concluded that *Q petraea* was a rather drought-tolerant species because of its ability to maintain significant daily transpiration rates even under decreasing soil water availability.

Seasonal time-course of predawn leaf water potential showed a similar pattern during the 2 yr of measurement: lower values were observed for sessile oak than for pedunculate during the periods of water shortage. We attributed this to a slightly higher transpiration rate in sessile than in pedunculate oaks. However, stomatal conductance was identical in both species. Higher sapflow in sessile oak could be explained by higher leaf area of individual trees. The total water extraction from 1.60 m depth was very similar in the vicinity of roots of pedunculate and sessile oaks. We also observed extraction from

deeper layers near sessile oaks (160 to 200 cm). These observations (higher leaf area and deeper soil water extraction) could help explain the slightly higher sapflow and lower ψ_{wp} in the 3 individuals from this species that we observed. But these observed differences may not be an intrinsic species-related feature. Rather, they could be due to the favorable competitive status of the sessile oak individuals in mixed stands containing pedunculate oaks. This competitive advantage of *Q petraea vs Q robur* in mixed stands of 30–60 yr has frequently been reported by forest practitioners and ecologists (Lévy *et al*, 1992).

We did not find any difference in maximal stomatal conductance (g_s) between species in well-watered trees. Restricted water supply had a strong effect on stomatal conductance: g_s was reduced by $\approx$ 70% between −0.6 and −2.0 MPa predawn leaf water potential (ψ_{wp}), with no interspecific difference. On the other hand, no clear relationships between g_s and neither the radiation nor the vapor pressure deficit could explain the large dispersion of g_s between 0 and −0.6 MPa. In fact, ψ_{wp} seemed to be a poor indicator of stress intensity when soil began to dry out, because it could not help explain the early decrease in leaf stomatal conductance. Instead of ψ_{wp}, the soil water potential measured in the 30 cm upper soil profile, which contains 60% of the fine roots, would probably be a better characteristic to relate to g_s. A recent hypothesis for stomatal regulation involves a hormonal signal from roots, which is influenced by soil water status. As reported by Schulze (1986) and Davies and Zhang (1991), soil water stress could trigger root signals stimulating stomatal reactivity. As a matter of fact, ψ_{wp} may not represent the water potential in the driest soil layers, from where root signals could proceed, but probably of the wettest and deeper rooting layers.

From this drought-induced course of stomatal conductance and total transpiration, we have concluded that the 2 studied species of oaks are water stress tolerant, and that no major difference between both exists under natural conditions.

However, under laboratory conditions, a difference in vulnerability to cavitation was observed between the species; *Q robur* is more sensitive than *Q petraea* (Cochard *et al*, 1992). Cavitation began when water potential reached −2.2 MPa, and a 50% of embolism was measured at −2.7 MPa for *Q robur* and −3.2 MPa for *Q petraea*. We showed a good agreement between the % loss of hydraulic conductivity measured under field conditions and those predicted by vulnerability curves when K_{max} was stable over the season. For pedunculate oak, we showed that K_{max} decreased, leading to an underestimation of the actual percentage of embolism. Two successive high pressure perfusions of samples did allow a complete dissolution of embolism (replaced the air by water) but the conductivity was not restored because of plugging of the vessels (tyloses, pit membrane occlusion, etc). The good stability of K_{max} between the first and the second flushes of high pressure reveals that air blockage of embolized vessels was not involved. The formation of tylosis as reported by Zimmerman (1979) that occurs in many trees at the end of the growing season and that occurs in *Q rubra* and *Q alba* (Cochard and Tyree, 1990) could presumably be responsible. A similar decrease in apparent K_{max} has been detected with potted saplings of *Q robur* during increasing drought (Simonin *et al*, 1994).

If embolism is directly dependent on leaf water potential, then leaf water potential is strongly related to another characteristic of hydraulic function: the leaf specific conductivity (LSC) of the petiole, which is calculated as the ratio of K_{max} and the leaf area. The consequences of differing LSCs on leaf water potential and probability of cavitation occurrence have been discussed by Jones and Sutherland (1991). We observed a slight difference in LSC between species: *Q robur* seemed to have lower LSC in petioles than *Q petraea* (data not shown) which could increase its susceptibility to cavitation.

In spite of a difference in vulnerability, both species reached approximately the same levels of losses in hydraulic conductivity (80%) under field conditions. In fact, dominant trees of *Q petraea* had lower leaf water potentials. It is worth noting that stomatal conductance was significantly reduced at ψ_{wp} = −0.6 Mpa, corresponding to ψ_{wm} = −2.0 MPa. This value is also the threshold for which embolism can significantly increase. Maximum stomatal closure occurred when ψ_{wp} = −1.5 MPa. At this time, ψ_{wm} = −3.0 MPa and the loss of hydraulic conductivity is close to 30%. Stomatal regulation was able to control the degree of embolism and to restrict it to this value for ≈ 1 month, despite decreasing soil water availability. Later on, with greater drought, stomatal regulation was not able to prevent a sharp increase of embolism. Loss of conductivity reached 80% within a few d. Such a situation is in agreement with the model suggested by Tyree *et al* (1988, 1989, 1991). It seemed surprising to us that such a large loss of conductivity in the petioles (and probably also in the youngest twigs) did not strongly affect the total sap flow of the trees. Total transpiration remained constant below − 2.5 MPa. This may be an illustration of the fact that the main resistance to liquid water flow from roots to leaves is probably located between the soil–root interface and the branches. As a consequence, strong increases in the minor resistance like that in petioles or twigs have only limited consequences on the total resistance to water flow (Tyree *et al*, 1994).

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