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Original article

Whole tree hydraulic conductance and water loss regulation in *Quercus* during drought: evidence for stomatal control of embolism?

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Summary — The water relations of 30-year-old *Quercus petraea* were studied for three consecutive growing seasons. Whole tree specific hydraulic conductances *(gL)* were computed from sap flow densities *(dF)*/leaf water potential (Ψ_{leaf}) relationships. *gL* was clearly reduced with the development of the drought. The decrease of *gL* with $\Psi_{predawn}$ was of an exponential type, ie, high variations of *gL* were found whereas $\Psi_{predawn}$ remained high and constant. These early variations of *gL* were most probably located in the soil-root compartment of the SPAC because no loss of hydraulic conductivity due to xylem embolism was detected in the crown of the trees. Although *gL* was reduced, Ψ_{midday} remained nearly constant and above −3 MPa throughout the drought period because dF_{midday} was also significantly reduced. As a consequence, a good linear relation was found between dF_{midday} and *gL*. Xylem embolism significantly developed in the petioles and twigs of *Q petraea* when Ψ_{midday} became less than −3 MPa. We argue that, because of changes in *gL*, *Q petraea* progressively adjusted its water loss throughout the drought development with the effect of maintaining Ψ_{midday} above the cavitation threshold. It is shown that if no water loss regulation had occurred, considerable tensions would have developed in the crown of these trees with predictable branch mortality due to runaway embolism.

Quercus petraea / drought / water relation / embolism / hydraulic conductance

Resumé — **Conductance hydraulique totale et régulation des pertes en eau chez *Quercus* en période de sécheresse : preuve d'un contrôle stomatique du développement de l'embolie ?**
Les relations hydriques de chênes sessiles agés de 30 ans ont été étudiées pendant trois saisons de végétation consécutives. La conductance hydraulique spécifique totale (gL) a été calculée à partir

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des relations densité de flux de sève (dF) / potentiel hydrique foliaire (Ψ_{leaf}). Nous avons noté une nette réduction de gL au cours du développement de la sécheresse. Exprimée en fonction du potentie hydrique de base ($\Psi_{predawn}$), la décroissance de gL a été de type exponentielle, c'est-à-dire que de fortes variations de gL ont été observées alors que $\Psi_{predawn}$ était élevé et constant. Ces variations précoces de gL étaient probablement localisées dans le compartiment racines-sol du SPAC en raison du faible développement de l'embolie dans le xylème. Bien que gL soit réduit, Ψ_{midday} est resté constant et au dessus de –3MPa tout au long de la sécheresse parce que dF$_{midday}$ fut réduit de façon importante. En conséquence une relation linéaire fut mise en évidence entre gL et dF$_{midday}$. Le taux d'embolie se développe de façon significative dans le xylème des pétioles et des rameaux feuillés lorsque Ψ_{midda} devient inférieur à –3MPa. Nous suggérons que, en raison des changements de gL, Q petraea ajuste progressivement ses pertes en eau ce qui a pour effet de maintenir Ψ_{midday} au dessus du seuil de cavi tation. Nous montrons qu'en l'absence de régulation des pertes d'eau des tensions xylémiques consi dérables se développeraient dans le houppier avec pour conséquence probable une mortalité impor tante des branches due au phénomène d'emballement de l'embolie.

Quercus petraea / sécheresse / relations hydriques / embolie / conductance hydraulique

INTRODUCTION

The physiology of the stomata is probably one of the most complex issues in plant physiology (Hinckley and Braatne, 1994). At the interface between the plant and the atmosphere, their aperture actively controls both water loss and the CO_2 uptake. The determinism of stomatal aperture and its function is still a matter of debate. Large stomatal conductances increase CO_2 uptake and productivity but also increase water loss, which can be damaging for plants particularly under drought conditions. The reason for this damage is that both high water loss and soil drought induce leaf water deficits. This results from the mechanism of water movement in plants. Water moves from the soil to the leaves driven by a negative potential gradient. This movement is simply and, in most cases, satisfactorily, described by an 'Ohm's law analogy' (Van den Honert, 1948): the water flow (F, kg s^{-1}) through a permeable segment (xylem conduits) causes a water potential drop ($d\Psi$, MPa) inversely proportional to the segment hydraulic conductance (K): $d\Psi = F/K$. Although the Ohm's law analogy is most applicable to a xylem segment, it has also been applied to the whole soil–plant water pathway:

$$\Psi_{soil} - \Psi_{leaves} = F/gl \quad [1]$$

where gl is an apparent hydraulic conduc tance of a plant considered as a unique seg ment; Ψ_{soil} is an averaged soil water poten tial; and Ψ_{leaves}, the averaged leaf wate potential when the total flow through the plant is F. When F is normalized by the sap wood area at breast height (sap flux den sity dF, dm^3•dm^{-2}•h^{-1}), a specific hydrauli conductance gL can be calculated. Equa tion [1] directly links the water losses, and therefore the stomatal aperture, to soil and leaf water deficits. The greater the wate flow, the greater the water tension devel oped in the distal part of the sap pathway Large water loss thus induces large wate deficit in the leaves which may impair plan physiology. The situation is more critica under drought conditions because gl and Ψ_{soil} are reduced, and a small water flov then induces very large leaf water deficit.

How water deficit affects tree physiolog is a complex issue. A possible action, tha has only recently been addressed, deal with the xylem dysfunction. Water deficit can induce xylem cavitation that disrupt sap transport to the leaves. If cavitation accumulate in the xylem, then the sap sup ply to the leaves can eventually stop, caus ing crown desiccation and mortality. Mod

els (Tyree and Sperry, 1988; Jones and Sutherland, 1991) suggest that stomata may play an important role in controlling the development of xylem embolism. Because cavitations develop when the xylem water potential becomes lower than a critical value (Sperry and Tyree, 1988), plants, by controlling their water losses, may maintain Ψ_{leaf} above the critical value (see eq [1]).

The objective of this paper is to test the hypothesis that sap flow and water losses are regulated during drought according to changes in whole tree hydraulic conductance in order to avoid development of xylem embolism. To test the hypothesis, we reanalyzed our data from a 3 year survey of water relations of mature oak trees in a forest stand partially submitted to drought. These data have been published in several papers (Cochard et al, 1992; Bréda et al 1993a, b) and reviewed by Dreyer et al (1993). The main results will be summarized later but readers can refer to the papers just mentioned for more details.

The predawn and midday leaf water potentials declined progressively during the drought development. Water potentials as low as −2 and −3.3 MPa were measured at the end of the dry period at predawn and midday, respectively. Stomatal conductances and daily maximum sap flow densities were considerably reduced by drought. The most important changes were noted at the beginning of the drought, ie, when $\Psi_{predawn}$ and Ψ_{midday} were still high. Whole tree apparent hydraulic conductance declined steeply at the beginning of the drought and then progressively during the development of the water shortage. These changes were reversible a few days after rehydration. Vulnerability curves established on petioles and 1-year-old twigs showed that the threshold water potential for cavitation is ca −2.7 MPa with 50% loss conductivity at −3.3 MPa. Close to 100% loss of conductivity (PLC) was noted at −4 MPa (see fig 4). Although the minimum daily

water potentials were very close to the threshold water potential inducing xylem embolism, the degree of embolism in petioles and the current year twigs remained low and increased significantly only at the end of the drought period when midday water potentials became lower than −3 MPa.

MATERIALS AND METHODS

Plant material and experimental plots

Experiments were conducted from 1990 to 1992 on 35-year-old, 16 m high, $Q\ petraea$ trees in the Forest of Champenoux, near Nancy, in east France (48°44'N, 6°14'E, altitude: 237 m). Each year, two groups of four trees each were chosen, one from a control that was well-watered by periodic irrigation, and one from a dry plot. The dry plot was 5 x 5 m in area, including about 15 trees, surrounded by a 1.4 m deep trench and covered by a watertight roof about 2 m above ground. At the end of the drought period, the plot was rewatered to field capacity. Two scaffolding towers gave access to the crown of the trees in each plot. A more thorough description of this site can be found in Bréda et al (1993b).

Measurements

Measurements took place during the growing seasons of the 3 consecutive years. Sap flow was continuously monitored by radial flow meters inserted in spring into the bole of the trees (Granier 1987). This device allows the measurement of the sap flux density (dF, $dm^3.dm^{-2}.h^{-1}$) along a 2 cm deep radial axis. The total sap flux through the bole ($dm^{-3}.h^{-1}$) can be estimated by multiplying dF by the sapwood area at the same height in the trunk. Leaf water potential was measured on two to five leaves per tree with a pressure chamber. Leaves were sampled on a weekly basis in the crown just prior to dawn (predawn water potential, $\Psi_{predawn}$) and at 1300 hours solar time (midday water potential, Ψ_{midday}). Daily courses of leaf water potential were also performed occasionally. Midday stomatal conductances, g_s, were measured on a weekly basis with a Li-Cor 1600

porometer (Li-Cor Inc, Lincoln, NE, USA) on five to ten sun-exposed leaves from different branches of the upper half crown of each tree. Whole tree specific apparent hydraulic conductances, gL, were estimated by the slope of the dF/Ψ_{leaf} daily regressions. These regressions were based on five to six points. gL was also calculated with a 'single-point' method according to the equation:

$$gL = -^* (dF_{predawn} - dF_{midday}) /$$
$$(\Psi_{predawn} - \Psi_{midday})$$

where $dF_{predawn}$ and dF_{midday} are the whole steady-state sap flow density through the tree at predawn (usually 0) and midday, respectively; $\Psi_{predawn}$ and Ψ_{midday} are the average leaf water potentials at the same time. Initial results demonstrated that the two methods yielded similar results ($n = 28$, $r^2 = 0.84$, slope = 1.1, not statistically different from 1 at $P = 0.05$) (fig 1). The second method being much less time consuming, most gL values shown in this paper were therefore computed with the predawn and midday values of dF and Ψ only. Days corresponding to incomplete leaf area expansion (late spring) or to heavily clouded days (low PET) were removed from the data set. Vulnerability of xylem conduits to embolism induced by water stress was assessed in 1-year-old twigs and petioles via the effect of cavitation on loss of hydraulic conductivity (Sperry et al, 1988). The procedure is described in detail by Cochard et al (1992). In short, 2- to 4-year-old branches were cut from the crown of control trees, brought to the laboratory and bench dehydrated. When branches reached a leaf water potential between –1 and –5 MPa, they were rehydrated for 30 min to reduce xylem tensions and 15 samples, 2–3 cm long, were excised under water. The initial hydraulic conductivity (K_{init}, kg m s^{-1} MPa^{-1}) was calculated by measuring the water flow through each sample (kg s^{-1}) when perfused with a 6 kPa head of distilled water. The maximum conductivity, K_{max}, was measured the same way after the samples had been perfused at 0.1 MPa for 20 min. The percent loss of conductivity was then computed as:

$$PLC = 100^*(1-K_{init}/K_{max})$$

The natural development of embolism was measured with the same technique on branches excised from the upper crown of each tree throughout the growing season.

RESULTS AND DISCUSSION

Hydraulic conductance and water loss

In figure 2, we represented for one representative drought tree and one control tree the seasonal patterns of the daily water potential/sap flow density relationships. By definition, the slope of these curves represent the whole tree apparent hydraulic conductance. In *Quercus petraea,* these relations were, in most cases, linear, indicating that the flow was always close to steady state (low tree capacitance) and that gL did not change during the day. It was therefore possible to compute gL values with flow/potential relationships. The sap flow has been found to be proportional to the water potential gradient in many species
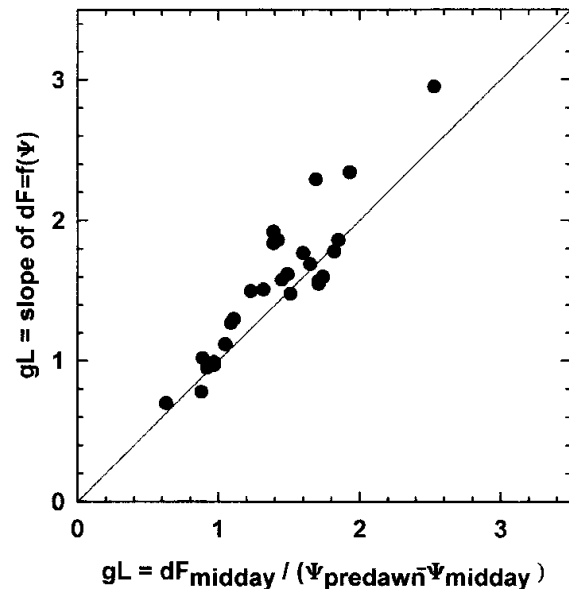

$$gL = dF_{midday} / (\Psi_{predawn} - \Psi_{midday})$$

Fig 1. Techniques to assess whole tree specific hydraulic conductances *(gL). gL* was calculated either as the slope of a linear regression between the daily variations in leaf water potential (Ψ) and sap flow density (dF) (y-axis) or as the ratio between the daily maximum flow density (dF$_{mid-day}$) and difference between the predawn and minimum leaf water potentials ($\Psi_{predawn} - \Psi_{mid-day}$). The two techniques yielded similar results ($r^2 = 0.84$, slope not different from 1 at $P = 0.05$). The latter method was preferred for its simplicity.

(Waring and Running, 1978; Cohen et al, 1983; Küppers, 1984; Reich and Hinckley, 1989; Granier and Colin, 1990) although earlier theoretical and experimental data also suggested nonlinear relations due to variable gL (Passioura, 1984). It can be seen that the relations remained unchanged for the control tree and that the maximum flow densities were comparable for the different days. The maximum transpiration rate was therefore not limited by climatic conditions for these days. For the stressed tree, drought induced a progressive drop of $\Psi_{predawn}$ (intercept on the x-axis) and to a lesser extent, Ψ_{midday}. gL was significantly reduced by drought. These variations were most likely located at the soil–root interface because gL came back to predrought values after rehydration and embolism developed in the petioles and twigs long after gL declined. Nevertheless, we cannot exclude embolism formation in the roots that may be more vulnerable than twigs (Sperry and Saliendra, 1994). dF_{midday} was considerably reduced during drought because of partial stomatal closure. Therefore, the changes in maximum sap flow densities occurred according to changes in gL and the conse-

quence was that the minimum water potentials always remained above ca −2.8 MPa.

Because the variations in $\Psi_{predawn} - \Psi_{midday}$ were limited during the drought, one should expect a relationship between the maximum sap flow density and gL. In figure 3, we plotted this relationship for our complete data set, ie, including data based on the single-point method. The relation found between these two variables was significant ($r = 0.76$, $n = 178$) and linear. The maximum transpiration rate is therefore correlated in *Quercus petraea* with the whole tree apparent hydraulic conductance. Correlation between water loss (or stomatal conductance) and hydraulic conductances have been reported for many herbaceous and ligneous species (Reich and Hinckley, 1989; Meinzer and Grantz, 1990; Brisson et al, 1993; Sperry and Pockman, 1993). These results suggest that water loss is permanently adjusted to the water transport capacity of a plant.

Two major questions arise from this behavior: i) what are the mechanisms triggering the stomatal closure, and ii) what are the functions of the stomatal regulation?

Fig 2. Typical summer pattern for the daily variations of sap flux density *(dF)* and leaf water potential (Ψ_{leaf}) for one control tree (closed symbols) and one water-stressed tree (open symbols). Different symbols correspond to different days. Error bars are one standard deviation. The variations were in most cases close to linearity which validated the computation of gL as reverse of the slope of these lines. gL remains constant along the summer whereas it was clearly reduced by drought. Although gL was reduced, the minimum daily water potentials remained above −2.8 MPa (dashed lines) due to a simultaneous reduction in the daily maximum sap flow density.
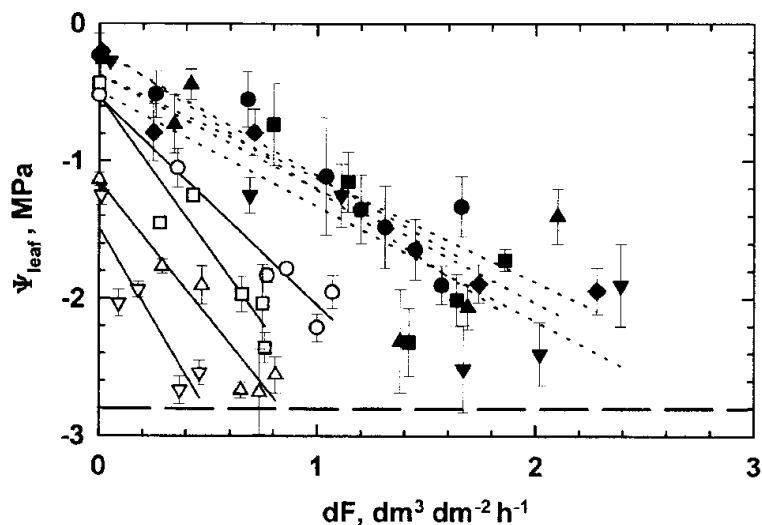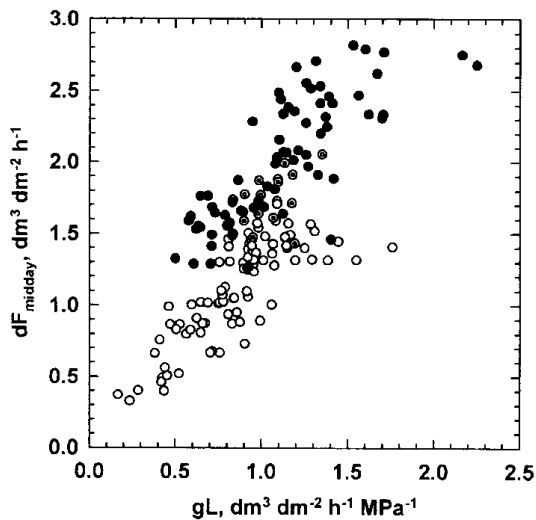
Fig 3. Daily maximum sap flow density ($dF_{mid-day}$) versus concurrent whole tree hydraulic conductance (gL) for control (closed circles), stressed (open circles) and rehydrated trees (dotted circles). dF_{midday} and gL were found to decrease linearly, which suggested that dF_{midday} was limited by the reduction in gL. After rewatering, gL and dF_{midday} came back to predrought conditions, indicating the reversibility of the phenomenon.

Stomata have long been supposed to respond to hydraulic signals caused by a decrease in leaf water potential, but more recent studies (Gollan et al, 1986; Zhang and Davies, 1989; Tardieu et al, 1992) have revealed the role of specific hormones (ABA) in the control of g_s during drought. Roots in the dry zones of the soil are producing ABA that provoke stomatal closure. An argument in favor of hormonal signals is that the stomatal conductance can be reduced independently of changes in leaf water status. This is the case in the first stage of a drought period (see earlier) or in split-root experiments (experiments where the roots are split into two compartments with different water regimes). In both situations, although the leaf water status is unchanged, the hydraulic functioning of the tree is largely modified due to large changes in gL. An hydraulic triggering signal for stomatal closure may still exist in plants (Malone, 1993).

Meinzer and Grantz (1990) addressed this issue in sugarcane. They suggested that the stomata respond to changes in gL via a possible effect of gL on the ABA production in the roots. Tardieu and Davies (1993) also proposed that in maize the sensitivity of the stomata to ABA depends on the current leaf water potential. Sperry and Pockman (1993) demonstrated that in *Betula*, stomata were also capable of reacting to changes in hydraulic conductances located only in branches, thus with constant root water status conditions. Clearly, the mechanisms of stomatal response to changes in gL deserve further study, and integration of both hydraulic and hormonal signals should be considered.

Stomatal control of embolism

The second issue may even be more puzzling for the physiologists. What limits the water losses of an oak tree during drought? The most often cited explanation is that critical tissue desiccation caused by low water potentials is what stomatal regulation has evolved to avoid. Tissue desiccation causes loss of turgor in the living cells which may impair growth and plant survival. In the short term, desiccation may cause xylem cavitation (Tyree and Sperry, 1988) and also compromise tree survival. The vulnerability to cavitation puts a functional limit to the xylem transport capacity. Any cavitation event reduces the xylem hydraulic conductivity and thus impairs the water transport to the leaves. Use of simple models (Tyree and Sperry, 1988) has shown that trees function close to the point of catastrophic xylem failure due to runaway embolisms. If the transpiration rate remains constant, then any decrease in xylem conductivity will decrease the water potential which causes further cavitation events and so on, until all the conduits are embolized. If this phenomenon occurs, then we can predict rapid desiccation

and eventually the death of the tissues situated apically from these xylem conduits. In this study, we did not determine the theoretical point of runaway embolism in the sense of Tyree and Sperry (1988) or Jones and Sutherland (1991), but we considered the point of xylem dysfunction, ie, when the degree of xylem embolism becomes significantly higher than the native state level. Our data on *Quercus petraea* revealed that this point corresponds to a xylem water potential (Ψ_{xylem}) of ca −2.5 MPa (fig 4). Because of large leaf-blade resistance in oaks (Tyree et al, 1993) Ψ_{leaf} underestimates Ψ_{xylem}, depending on the evaporative flux density. We estimated that when Ψ_{leaf} = −2.8 MPa, Ψ_{xylem} is close to the point of xylem dysfunction (−2.5 MPa). The fact that Ψ_{leaf} remained for a very long period above −2.8 MPa because dF_{midday} was reduced (fig 2) and that g_s was less than 10% of its maximal values when Ψ_{midday} was close to −2.8 MPa (fig 4) suggested to us that in *Quercus petraea* the stomatal closure is protecting the xylem from embolism development. To

explore this hypothesis, we constructed a simple model relating dF to gL and Ψ based on equation [1]:

$$dF_{cavitation} = gL^*(\Psi_{predawn} - \Psi_{cavitation})$$

where $dF_{cavitation}$ is the critical maximum sap flow density that for any given values of $\Psi_{predawn}$ and gL induced a minimum leaf water potential equal to the point of xylem dysfunction ($\Psi_{cavitation}$ = −2.8 MPa). In figure 5, we plotted the relationship between the actual dF_{midday} and the predicted $dF_{cavitation}$. It is clear from this graph that dF_{midday} was in all cases very close to $dF_{cavitation}$, indicating that trees were operating close to the point of xylem dysfunction. As drought developed, $dF_{cavitation}$ decreased because both $\Psi_{predawn}$ and gL decreased; nevertheless, dF_{midday} was adjusted and remained below $dF_{cavitation}$ for most of the trees. We computed that for the driest trees, the dif-
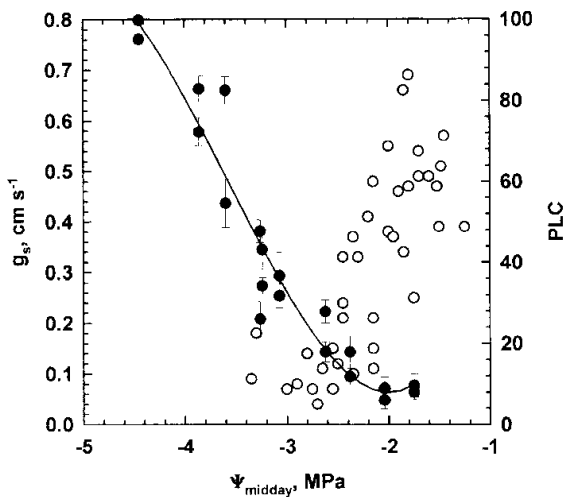
Fig 4. Percent loss hydraulic conductivity (PLC) due to xylem embolism (closed circles) and midday stomatal conductance (g_s) (open circles) versus leaf water potential at midday (Ψ_{midday}). Vertical error bars represent one standard deviation. Embolism significantly increased in petioles and twigs when Ψ_{leaf} became lower than −2.7 MPa, the point where the g_s was reduced to about 10% of its maximal value.
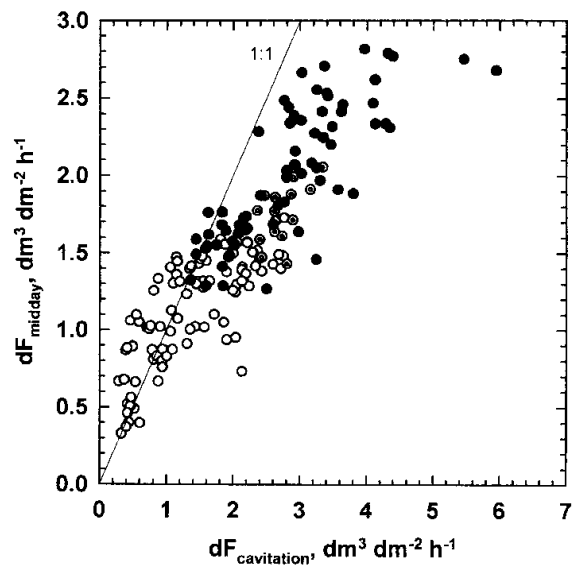
Fig 5. Actual midday sap flow density (dF_{midday}) versus theoretical sap flow density ($dF_{cavitation}$) inducing xylem embolism (see text for details). Symbols as in figure 3. dF_{midday} was found close to $dF_{cavitation}$, suggesting that the trees were functioning close to the point of xylem dysfunction. As drought developed, dF_{midday} was reduced but remained for a long time below $dF_{cavitation}$. Only at the end of the drought period did dF_{midday} became higher than $dF_{cavitation}$.

ference between dF_{midday} and $dF_{cavitation}$ represented less that a few percent of the dF_{midday} of the control trees. It can be noted that for some droughted trees, dF_{midday} became higher than the predicted $dF_{cavitation}$. Xylem embolism should occur under these conditions according to our hypothesis. Our seasonal survey of xylem embolism revealed that cavitation drastically developed only in trees that did not maintain Ψ_{midday} above $\Psi_{cavitation}$ (positive x values in fig 7). Stomata may not be able to respond to changes in gL after a prolonged period of drought, as suggested by Sperry and Pockman (1993).

A second way to illustrate the critical role of the stomata in the control of xylem embolism is to compute a theoretical minimum water potential, Ψ_{min}, that would occur if the no regulation took place, ie, if the transpiration of the stressed trees was set equal

to the transpiration of the control trees ($dF_{control}$) all through the drought period:

$$\Psi_{min} = \Psi_{predawn} - dF_{control}/gL$$

In figure 7, we expressed Ψ_{min} and Ψ_{midday} as a function of gL. It is clear from this graph that considerable tensions would have occurred in the leaf xylem of the drought trees in the absence of regulation. We can thus predict that because of these tensions and because of runaway embolism, the degree of embolism would have soon reached 100%. Throughout these 3 consecutive years, stomatal closure in *Quercus petraea* contributed to the maintenance of xylem integrity and protection against damage caused by vessel cavitation. This behavior probably enhances the fitness and the survival of this species.
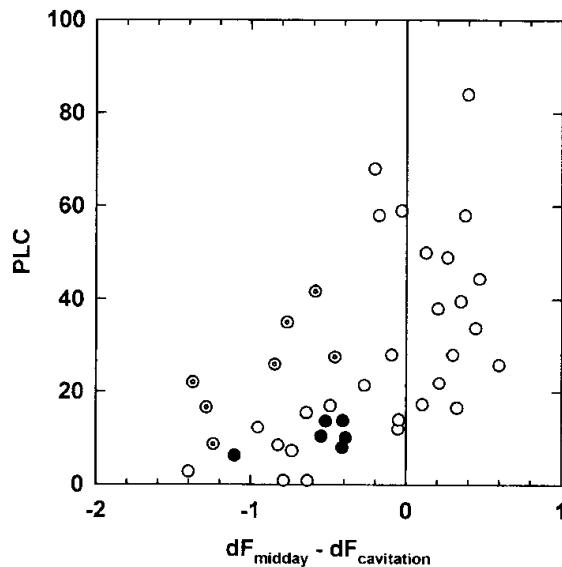

Fig 6. Measured degree of embolism in petioles versus difference between actual dF_{midday} and calculated $dF_{cavitation}$. Symbols as in figure 3. According to our model, when dF_{midday} becomes higher than $dF_{cavitation}$ (positive values on x-axis), then embolism should develop. Our predictions are consistent with the measured degrees of embolism. Note that due to the irreversibility of embolism in oak, PLC in rehydrated trees remained high although dF_{midday} became lower than $dF_{cavitation}$ after rehydration.

CONCLUSION

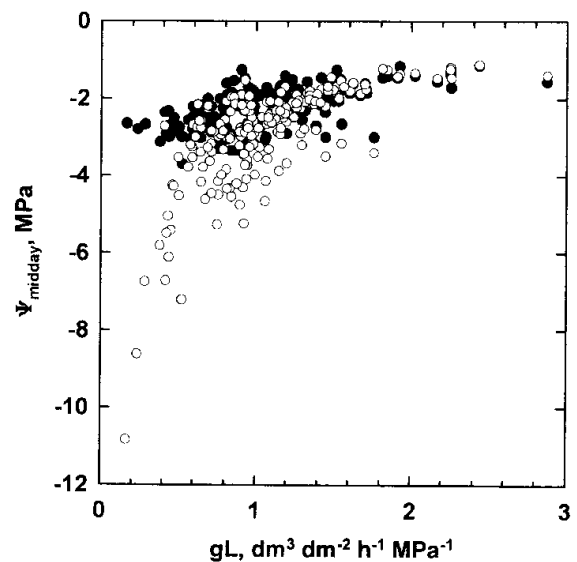Many authors have already pointed out the apparent correlation between the stomatal

Fig 7. Actual (closed circles) and theoretical (open circles) midday leaf water potentials (Ψ_{midday}) versus gL. The theoretical Ψ_{leaf} is the potential that would be generated in the absence of water loss regulation.

conductance and the water transport capacity of a plant. In this paper, we give further evidence for this co-functioning in *Quercus petraea*, but we further argue that this regulation plays a major role in controlling the development of xylem embolism by maintaining the minimum water potential above the threshold potential for xylem dysfunction. The maximum theoretical sap flow density and thus the degree of stomatal regulation in *Quercus petraea* can therefore be inferred from the water transport capacity of the whole tree *(gL)* and the xylem vulnerability to embolism induced by water stress. The mechanisms of stomatal response to change in hydraulic conductance is unknown and may involve both an hormonal and an hydraulic signal. Whatever the mechanism, our data demonstrate that it is extremely accurate because any minor deviation from the actual flow value would have led to catastrophic xylem dysfunction. Data on the hydraulic functioning and dysfunctioning of plants may therefore generate significant progress in the understanding of whole tree water relations.

ACKNOWLEDGMENTS

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