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Review article

Summer and winter embolism in oak: impact on water relations

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Summary — In this paper we review vulnerability to embolism caused by drought and freezing in six species of oak (*Quercus*). The xylem pressure potential that induces 50% loss hydraulic conductivity ranges from –2.5 to –6.0 MPa for the species reviewed and correlates with other measures of drought tolerance in oaks. The probability of vessel dysfunction increases with vessel size for both drought- and freezing-induced embolism. The impact of embolism is a reduction in hydraulic conductivity in the vascular system. We conclude that embolism plays little role in the drought tolerance of oaks since drought-induced embolism occurs at more negative water potentials than are known to cause damage (eg, reduced growth) or mortality. Nevertheless, vulnerability to embolisms probably explains species distributions between wet and dry sites or may explain the evolution of stomatal physiology. Oaks seem to operate close to the point of xylem dysfunction, but oaks protect against embolism by stomatal regulation which keeps water potentials above that causing 'run-away' embolism. In conclusion, vulnerability to summer embolisms correlates with other measures of drought tolerance of oak species but significant summer embolisms are generally avoided. On the other hand, frost-induced embolism may explain species distributions in cold climates.

***Quercus* spp / embolism / water relations / hydraulic conductance**

Résumé — Embolie estivale et hivernale chez les chênes : conséquences sur les relations hydriques. *Cet article fait la synthèse des données sur la vulnérabilité à l'embolie causée par stress hydrique et thermique de six espèces de chênes* (Quercus). *Le potentiel hydrique induisant 50 % de perte de conductivité hydraulique varie de –2,5 à –6,0 MPa selon les espèces analysées et est corrélé à d'autres indices de tolérance à la sécheresse chez les chênes. La vulnérabilité des vaisseaux à la sécheresse et au gel augmente avec leur taille. L'embolie a pour conséquence de réduire la conductivité hydraulique du système vasculaire. Nous avons conclu que l'embolie joue un rôle mineur dans la tolérance à la sécheresse de chênes puisque l'embolie se développe à des potentiels hydriques plus*

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négatifs que ceux induisant des dommages (par exemple réduction de la croissance) ou de la mortalité. Néanmoins, la vulnérabilité à l'embolie pourrait expliquer la distribution des espèces entre les régions sèches et humides et peut expliquer l'évolution de la physiologie des stomates. Les chênes semblent fonctionner près du point de dysfonctionnement du xylème, mais ils se protègent du risque d'embolie grâce à une régulation stomatique qui permet de maintenir le potentiel hydrique au-dessus du point «d'emballement» de l'embolie. En conclusion, la vulnérabilité à l'embolie estivale est corrélée à d'autres mesures de tolérance à la sécheresse chez les chênes, mais des degrés importants d'embolies estivales sont généralement évités. D'autre part, l'embolie induite par le gel pourrait expliquer la distribution des espèces sous climats froids.

Quercus *spp / embolie / relations hydriques / conductance hydraulique*

INTRODUCTION

During the growing season, water is lifted up into the leaves by less-than-atmospheric pressure created in the leaf xylem by transpiration. Our current understanding of the mechanism of sap ascent is based on the cohesion theory usually ascribed to Dixon (1914), and a useful biophysical review of the theory can be found in Pickard (1981) and Tyree et al (1995). Briefly the process can be described as follows. Evaporation from cell wall surfaces inside the leaf causes the air-water interface to retreat into the finely porous spaces of the cell walls and places the mass of water behind it under negative pressure. This negative pressure is physically equivalent to a tension (a pulling force) that is transmitted to soil water via a continuous water column (Van den Honert, 1948) in the xylem. The vascular system is vulnerable to dysfunction because any break in the column in a conduit drains the conduit of water and necessarily disrupts further water flow.

A break in the water column (a cavitation event) ultimately results in dysfunction of the vascular transport pathway. A cavitation occurs when a void of sufficient radius forms in water under tension. The void is gas filled (water vapor and some air) and is inherently unstable, ie, surface tension forces will make it spontaneously collapse unless the water is under sufficient tension (negative pressure) to make it expand. Embolisms that persist for days to months can form by drought-induced or by freezing-induced events. The purpose of this paper is to summarize what is known about both kinds of events and to examine whether these events can explain differences in physiological performance (drought resistance or freezing resistance) between *Quercus* spp or between *Quercus* and other tree taxa.

DROUGHT-INDUCED EMBOLISM

Method of measurement

Cavitation events can be detected acoustically or hydraulically. Cavitation events are accompanied by a rapid release of tension in the water column with a half time of approximately 1 µs. The rapid tension release produces a range of ultrasonic and audio sound emissions (Milburn, 1973; Tyree and Sperry, 1989). In some cases the number of acoustic emissions may be proportional to the loss of hydraulic conductance caused by cavitation (LoGullo and Salleo, 1993). The advantage of acoustic detection is that it is nondestructive. But hydraulic detection gives more information on the cumulative impact of cavitation to the water relations of plants.

Hydraulic detection involves measuring hydraulic conductance of stem segments before and after removal of embolisms. Briefly, stem segments are excised under water to prevent sucking air bubbles into cut vessels. Segments from 0.02–0.3 m long are connected to a water-filled conductivity manifold. A pressure difference (ΔP) from 2 to 10 x 10^{-3} MPa is applied across the stem segment of length L (m) and the resulting flow across the stem, w (kg s^{-1}), is measured. An initial hydraulic conductivity $K_i = wL/\Delta P$ is computed. Then degassed water is flushed through the sample at higher pressure differences of 0.1–0.2 MPa. Usually one to three flushes of 10 min duration is enough to dissolve all embolisms and restore the hydraulic conductivity to a maximum value (= K_m). Percent loss hydraulic conductivity due to embolisms (PLC) is calculated from

$$\mathrm{PLC} = 100(1 - K_i/K_m)$$

Different species have different vulnerabilities to PLC due to drought-induced cavitation. A water stress of –3 MPa might cause a 50 PLC in one species and only a 10 PLC in another. A vulnerability curve is a plot of PLC versus the water potential that induced the measured PLC. A vulnerability curve can be used to compare the vulnerabilities of different species to drought-induced loss of hydraulic conductivity due to embolism. Vulnerability curves are measured by dehydrating stems to a measured xylem pressure potential, Ψ_{XP}, to induce cavitation events. Cavitated vessels soon fill with air to cause a more permanent blockage of water flow (an embolism). The stems are usually returned to $\Psi_{XP} = 0$ by cutting them under water and the PLC determined. Different stems are dehydrated to different Ψ_{XP} values to obtain resulting levels of PLC. Exactly how the stem segment is dehydrated does not seem to affect the vulnerability curve. Dehydration of whole plants by withholding irrigation has the same effect on PLC as dehydrating excised branches, provided stem segments are cut far enough away from the cut end to avoid sampling vessels cut open when the stems were excised (Sperry et al, 1988; Tyree et al, 1992).

Vulnerability curves of* Quercus *spp and other measures of drought resistance

Vulnerability curves for drought-induced embolism have been measured on six species of *Quercus*. Most measurements have been done on current-year stems (fig 1). When vulnerabilities of petioles are compared they are usually as vulnerable or more vulnerable than the stems (Cochard et al, 1992). A more vulnerable petiole allows stems to avoid cavitation by a leaf-shedding mechanism (Tyree et al, 1993a). The water potential that induces 50 PLC (Ψ_{50}) is a useful measure of relative vulnerability of different species. Ψ_{50} can range from –2.3 MPa in *Q rubra* to –6.0 MPa in *Q ilex*. (A vulnerability curve has also been measure on *Q gambelii* by Sperry and Sullivan [1992];

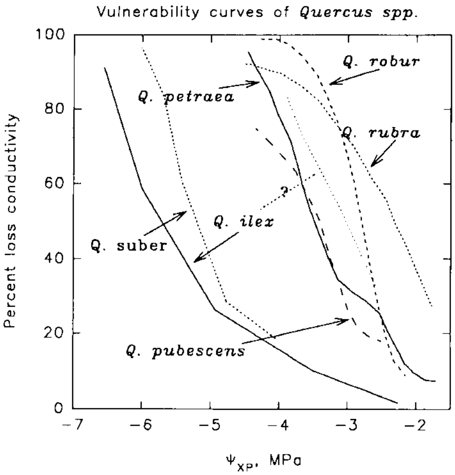

Fig 1. Vulnerability curves for six species of oak. *X*-axis is the xylem pressure potential needed to induce the percent loss hydraulic conductivity on the *Y*-axis.

but the interpretation is complicated by a high native-state embolism in 2- and 3-year-old stems that cavitate during winter and do not form tyloses. If the native embolism is subtracted, then Ψ_{50} is about –4.5 MPa.) Not enough vulnerability curves are available to know if there is a general correlation between vulnerability to cavitation and other measures of drought tolerance but so far such a correlation holds (except for the data on *Q ilex* from LoGullo and Salleo [1993], which could not be reproduced by us, ie, see the two different vulnerability curves marked *Q ilex* in fig 1).

The most complete set of data permits comparison of *Q petraea* to *Q robur;* see table I. Silvicultural experience has shown *Q robur* to be more vulnerable to drought than *Q petraea*. This correlates with a number of other physiological estimators of drought tolerance. When comparing *Q robur* to *Q petraea*, we find that it is more vulnerable to cavitation, stops growth at less water stress, has a higher mortality rate after a drought cycle, and has a higher resistance to water flow in shoots of 20–25 mm basal diameter. (The higher resistance to water flow will make *Q robur* reach lower Ψ at any given transpiration rate than *Q petraea*.)

In detailed studies of cavitation in *Q ilex*, some interesting relationships were found (LoGullo and Salleo, 1993). Large diameter vessels were found to be much more vulnerable to cavitation than small diameter vessels; this is significant because large diameter vessels are much more efficient conductors of water than small vessels. A moderate level of water stress (Ψ_{XP} = –2.7 MPa) resulted in a 33 PLC but was largely reversed by a 4 mm precipitation event, eg, 24 h later, the PLC was just 8%. Larger losses of conductivity caused by $\Psi_{XP} < -3.1$ MPa were much less reversible by 4 mm rain events. Reversal of embolisms in any plant probably requires a period of positive or near-positive pressures in vessels; readers interested in these issues should consult Tyree et al (1995) and references cited therein.

Can vulnerability to cavitation explain differences in drought tolerance among Quercus *spp?*

Although the vulnerability to cavitation of *Quercus* spp may be consistent with other measures of drought resistance, there probably is more involved. Any process that caused a loss of conductivity of the soil-to-leaf hydraulic conductance would cause increased water stress at any given transpiration rate. Decreased leaf water potential (Ψ_{leaf}) will correspond to decreased growth, stomatal conductance and net assimilation (Vivin et al, 1993). The rela-

Table I. Measures of drought resistance for *Q robur* (QR) and *Q petraea* (QP).

QR	*QP*	*Reference*	*Quantity*
–2.7	–3.3	1	Ψ_{XP} needed to induce 50 PLC, MPa
–1.8	–1.8	2	Ψ for stomatal closure, MPa
–2.0	–2.5	2	Ψ at which growth effectively stops, MPa
18%	5.6%	2	Death rate after drought stress to predawn Ψ of –5 MPa
3 350	2 170	3	Stem hydraulic resistance (22 mm basal diameter) (MPa s m^2 kg^{-1})

References: 1 = Cochard et al (1992); 2 = Vivin et al (1993); 3 = Tyree et al (1993b).

tionship between Ψ_{leaf} and hydraulic conductance is:

$$\Psi_{leaf} = -E(1/K_R + 1/K_L + 1/K_V) + \Psi_{soil}$$

where K_V is the vascular conductance from minor roots to leaf veins, K_R and K_L are the nonvascular conductances of the roots and leaves, respectively.

Cavitation events cause a loss of conductivity in K_V, but changes in K_V do not appear to be significant in comparison to the loss of conductivity in K_R and/or K_L. A common presumption is that most of the loss of K_V is probably confined to the apex of the vascular system (Zimmermann, 1983) where Ψ_{XP} is most negative. A typical 30 PLC in current-year stems might translate into just a 5 PLC in the entire vascular system. Furthermore, leaf resistance to water flow ($1/K_L$) is much more than the vascular resistance ($1/K_V$), making the impact of cavitation even less on Ψ_{leaf} (Tyree et al, 1993).

Soil-to-leaf conductances were reported to fall to half or a third their original values as predawn Ψ_{leaf} fell from 0 to –2 MPa in *Q petraea*. This occurred during a severe, imposed drought, but only limited loss of conductance in twigs and petioles was observed (consistent with midday values of Ψ_{leaf} and measured vulnerability curves). Changes in soil-to-leaf conductance of similar magnitude have been reported in other *Quercus* spp (Reich and Hinckley, 1989; Ni and Pallardy, 1990). Most of the change in soil-to-leaf conductance during drought is thought to be confined to the root and/or soil part of the pathway. Extensive embolism in the root vessels might account for the two- or threefold change in conductance if roots are more vulnerable to cavitation than shoots. There is growing reason to believe that roots are more vulnerable than shoots to cavitation (Sperry and Saliendra, 1994), so the possible impact of changes in K_V on the total plant conductance during drought needs to be evaluated more carefully. But no work has been done on vulnerability of oak roots to cavitation or to localize the site of conductance change in roots.

Even 100 PLC to stems of *Quercus* spp may be nonlethal. When *Q robur* and *Q petraea* saplings where dehydrated to –5 MPa (table I), all stems should have suffered 100 PLC, yet a large fraction of the trees survived over winter (Vivin et al, 1993). While most stems died, there was resprouting from roots and some axial buds. This is consistent with the normal behavior of *Quercus* over winter, ie, it will be seen below that *Quercus* spp suffer a high PLC due to freezing and survival of the tree depends on the formation of a new ring of sapwood before leaf flush in spring.

Nevertheless, there is a striking correlation between vulnerability curves and general perceptions of drought tolerance from silvicultural literature, ie, the arid-zone species (*Q ilex* and *Q suber*) are less vulnerable than mesic-zone species (*Q robur* and *Q robur*). So differences in vulnerability appear to be selected over evolutionary time-scales and thus may be of biological importance. The mode of selection may be at the seedling establishment stage in the life cycle of oaks. The vulnerability to cavitation of a seedling is likely to determine the chance of survival during a drought.

Vulnerability to cavitation and stomatal physiology may coevolve in oaks (Cochard et al, 1996). Cochard found that the reduction in soil-to-leaf conductance during a prolonged drought in *Q petraea* caused a reduction in maximal transpiration rates. The transpiration rates reduced just enough to maintain the minimum Ψ_{leaf} above the cavitation threshold. Computer simulations demonstrated that lack of stomatal regulation would have caused high loss of conductance in twigs and petioles as soon as drought developed. Thus the vulnerability curve of the species appears to put a selective constraint on the evolution of the stomatal physiology (a theoretical limit to maximum transpiration), which in turn limits the ultimate gas exchange and productivity of oaks.

FREEZING-INDUCED EMBOLISM

Freezing should induce embolisms, because air is not soluble in ice. So when water freezes, air comes out of solution. If water is saturated with air at 0 °C when it freezes, approximately 2.8 mL of air will come out of solution for every 100 mL of frozen water. This air will redissolve in the water when the ice melts if no xylem tension exists, but if the xylem tension is more than a small critical value (usually 10–20 kPa), then the bubbles will expand to make the conduit fully embolized and dysfunctional.

Cochard and Tyree (1990) were the first to demonstrate large losses in stem and petiole conductances (80–95 PLC) in *Q rubra* and *Q alba* immediately following a frost event in October prior to leaf abscission. Similar studies have been done with much more care by LoGullo and Salleo (1993) on *Q ilex*. In freezing experiments on nondormant seedlings frozen to temperatures of −1.5 to −11 °C, the PLC was found to increase with decreasing temperature and with increasing vessel diameter at any given temperature. In general, large diameter vessels were more prone to freezing-induced dysfunction than small vessels when comparing diverse taxa.

Sperry and Sullivan (1992) prestressed branches to various Ψ_{XP} values by dehydrating excised branches in a laboratory. They were enclosed in plastic bags to prevent further water loss. The prestressed branches were put in a freezer and frozen to −20 °C and then thawed at room temperature. The prior stress required to induce 50 PLC after freezing (Ψ_{50F}) decreased with increasing vessel or tracheid volume in five species of trees; see figure 2.

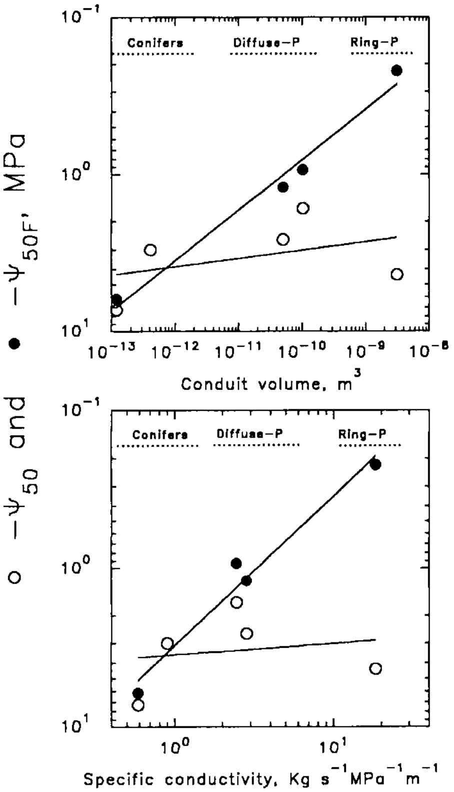

Fig 2. Relationship between xylem tension and loss of conductivity. Open circles are tension (negative Ψ_{XP}) needed to induce 50 PLC = Ψ_{50}, closed circles are tension before a freeze, required to induce 50 PLC = Ψ_{50F}. The upper plot shows the relationship with conduit volume and the lower plot shows the relationship with specific conductivity. The lower curve suggests a trade-off between vulnerability to freezing-induced loss of conductance and specific conductivity of wood. (Replotted from Sperry and Sullivan, 1991.)

The level of prior Ψ_{XP} could not influence the amount of air coming out of solution upon freezing, the same amount of air will come out regardless of the initial conditions because the solubility of air in ice is very low compared to water at 0 °C. Since the samples frozen were not frost tolerant, many living cells must have died and this would alter Ψ_{XP} after the freeze and thus the capacity of the cells to take up water. The capacity to remove water from vessels following a thaw is what will determine the PLC. If no air dissolved after the thaw, only 2.8% of the tissue volume would be occupied by air (= the volume fraction of air in solution at the time of the freeze). Only if these bubbles are expanded to fill the entire conduits would we expect values of 50 PLC or more. Although the level of tension *after* the thaw was unknown in these experiments, the results do suggest that large conduits are more prone to freezing-induced dysfunction than small conduits.

Why should large conduits be more prone to freeze-induced dysfunction? It probably has something to do with how long it takes air bubbles to dissolve rather than the tension when the ice first forms. This is because bubbles have to dissolve before the onset of a critical tension causing them to expand. The physics of air bubble dissolution is now well understood (Pickard, 1989; Tyree and Yang, 1992; Yang and Tyree, 1992). An analysis of the kinetics of bubble dissolution reveals that the time it would take for a bubble to dissolve increases approximately with the square of its initial diameter. If many small bubbles were formed when ice melted and if the bubbles were the same size regardless of size of the conduit, then conduit size may not influence freezing-induced dysfunction. However, Ewers (1985) studied bubble formation while freezing and thawing water in small glass capillary tubes and observed that bigger bubbles formed in large diameter tubes than in small tubes and that they took longer to redissolve in big versus small tubes. It seems likely that the same will happen in xylem conduits.

More studies are needed of frost-induced xylem dysfunction. Such studies may reveal why oaks tend to be excluded from cold climates and/or regions subject to late frosts after leaf flush.

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