OAK TREES UNDER DROUGHT CONSTRAINTS:
ECOPHYSIOLOGICAL ASPECTS

E. DREYER, A. CRANIER, N. BRÉDA, H. COCHARD, D. EPRON and G. AUSSENAC

Laboratoire de Biclimatologie et d’Ecophysiologie Forestières,
INRA Nancy, Champenoux, France

SUMMARY

This review presents recent results and analyses of the physiological responses of oak trees to drought stress. Drought is probably one of the major decline inducing environmental constraints. Mesophytic oaks display in general a rather good tolerance to drought, as they present a rather low susceptibility to cavitation, and are able to maintain stomata open till low water availability. Their photosynthetic apparatus seems to be well protected against photoinhibition. The ecological consequences of these features are discussed.

RIASSUNTO

Querce sotto stress idrico: aspetti ecofisiologici.

Questo articolo presenta i risultati e le analisi più recenti delle risposte fisiologiche delle querce sotto stress idrico. La seccità è probabilmente uno dei più importanti fattori che inducono il deterioramento delle piante. Le querce mesofitiche hanno in genere un comportamento tollerante alla seccità, con una bassa suscettibilità alla cavitation e con la capacità di mantenere aperti gli stomi anche in condizioni di scarsa disponibilità idrica. Il loro apparato fotosintetico sembra essere ben protetto contro la fotoinibizione. Le conseguenze ecologiche di tali caratteristiche vengono discusse.

INTRODUCTION

Several periods of dieback have affected many different oak stands (Quercus petraea (Matt.) Liebl. and Q. robur L. in Central
Europe, *Q. cerris* L., *Q. robur* L., and *Q. petraea* Willd. In southern Europe, *Q. ilex* L., *Q. rubra* L., and many others in North America) described to epidemic diseases like oak wilt due to *Ceratocystis fagacearum* in northern America. Many other pathogens were suspected to play important roles in these decline processes; but nevertheless, the majority of authors stress the potential role of climatic hazards as winter or late spring frosts, or drought in the onset of decline.

In France, important periods of decline concerned *Q. petraea* and *Q. robur* and were recorded during the 20s, the late 40s, the late 70s and beginning 90s (Delaunay, 1983; Landmann et al., 1992). The onset of many of these decline processes could be Tronquays (Central France), or in the hills of Béarn (SW France) showed 1976 (Becker and Lévy, 1983; Durand et al., 1985). An interesting fact, more thorough ecological surveys of the stands undertaken since higher mineral nutrient availability than *Q. petraea*. Moreover, in demonstrating that for some reason, *Q. robur* had probably been why it may suffer more from periods of environmental constraints trees illustrated the dependence of growth on climate conditions variations in competitive status, these authors showed that the basal North Eastern France was very sensitive to climatic constraints, and model including monthly precipitation and temperature from current and previous years explained satisfactorily the interannual variability of oak, the mean growth of the studied oak. Furthermore, the increase in BAIC was significantly greater for *Q. petraea* than for *Q. robur*.

Because of these strong effects of climatic hazards, and particularly drought, on oak growth, it was felt necessary to undertake a detailed survey of the ecophysiological reactions to drought of different oak species. This review considers the comparative ecophysiology of a broad range of species from diverse geographical origins.

**Drought and oaks: a few definitions**

Reactions of trees to drought are in a first stage best analysed at a whole tree level, by a description of effect on growth, water relations and primary productivity. The general model suitable for that purpose has been frequently described (see Whitehead and Jarvis, 1981; Hinchley et al., 1983). Drought is primarily a depletion of soil water, which induces a decrease in soil water potential. This decrease in soil water potential is often detected via its effect on predawn leaf water potential (which approximates the equilibrium value in the soil-plant continuum). Water transport through trees consists of a liquid path from soil to leaves followed by a vapour path to the atmosphere.

In the liquid path, the flux may be described by the Ohm analogue as:

\[
F = (\Psi_{\text{soil}} - \Psi_{\text{leaf}}) / \Sigma R
\]

where \( \Psi_{\text{soil}} \) = soil water potential (MPa), \( \Psi_{\text{leaf}} \) = leaf water potential (MPa), \( F \) = total flux of water through the tree (mmol m\(^{-2}\) s\(^{-1}\)), \( K \) = hydraulic resistance to water flow from soil to leaves; the hydraulic conductance is: \( g_{\text{soil}} = 1/R \) (mmol m\(^{-1}\) s\(^{-1}\)).

In the vapour path, the flux is described using Fick's law:

\[
E = g_e (w_i - w_a)
\]

where \( E \) = transpiration (generally expressed as a flux density on a leaf area basis (mmol m\(^{-2}\) s\(^{-1}\)), \( g_e \) = total conductance to water vapour (mmol m\(^{-2}\) s\(^{-1}\)), \( w_i, w_a \) = molar fractions of water vapour in the intercellular spaces and in the atmosphere.

In the steady state and on a daily scale, \( E \cdot LA = F \) (where \( LA \) is the total leaf area); i.e. water transfer in trees is conservative. In this
case, expression 1 may also be written as:

\[
\Psi_{\text{leaves}} = \Psi_{\text{soil}} \cdot \frac{LA}{E^{*}(\Sigma R)} = \Psi_{\text{soil}} \cdot E'/E_L
\]  \hspace{1cm} (3)

where \( E' \) is a leaf specific hydraulic conductance (i.e. \( E' = g_{\text{leaf}}/LA \)).

Expression 3 nicely demonstrates the strong interactions between changes in hydraulic resistances (or leaf specific stomata is central in this regard, as it helps to control \( E \) and therefore soil to leaves (\( g_e = 1/(\Sigma R) \)) and may be applied easily if we use the predawn leaf water potential (\( \Psi_{wp} \)) as an estimate of \( \Psi_{\text{soil}} \).

Changes in \( g_e \) affect the net influx of CO\(_2\) as:

\[
A = g_e (c_a - c_i)
\]  \hspace{1cm} (4)

\( A = \text{net CO}_2\text{ assimilation rate (\mu mol m}^{-2}\text{s}^{-1})\); \( g_e = \text{leaf conductance to CO}_2\text{ (mmol m}^{-2}\text{s}^{-1}) = g_m/1.6; \)
\( C_a, C_i = \text{mole fractions of CO}_2\text{ in the intercellular spaces and in the atmosphere.} \)

Finally, it should be emphasized that the transport of CO\(_2\) to the chloroplast is opposed to a final set of resistance leading to a mesophyll conductance \( g_m \) used in equation 5:

\[
A = g_m (c_i - c_e)
\]  \hspace{1cm} (5)

\( C_e = \text{mole fraction of CO}_2\text{ in the chloroplast stroma; this discrimination or chlorophyll a fluorescence, Loreto \text{ et al.} (1992).} \)

These models have been much refined to take into account water storage in trunks, ramifications, or the three-dimensional structure of the tree and canopy. Boundary layer effects may also be of simple form presented here is nevertheless useful for analysing the primary effects of drought on water relations and photosynthesis at a single tree level, which will be the scope of this review.

Effects of drought on growth and water relations of oak trees

As has been clearly demonstrated by the dendrochronological studies, the radial increment of \( Q. \) robur and \( Q. \) petraea trees is strongly affected by climatic factors. Availability of water probably plays a major role. Other factors, such as low temperatures seem to be of secondary importance.

Direct and quantitative analyses of the effects of soil water depletion on shoot and root growth of oak trees are rather rare. In fact, such analyses are difficult due to the rhythmic behaviour of oak shoot growth (Champagnat, 1989), which occurs in very variable flushes, i.e. 1 to 3 in adult trees and 2-5 in young saplings grown with optimal nutrient and water supply.

Nevertheless, Aussenc and Lévy (1983) and more recently Vivier \text{ et al.} (1993) evidenced a marked decrease in the potential shoot elongation of 8 years old seedlings as soon as the predawn water potential decreased to levels near -1.0 MPa. Only very limited elongation could be observed with greater stresses (ill 2.0 MPa). An analogous strong decline of shoot growth was described by Screll (1990) for 3 month-old seedlings, at even higher \( \Psi_{wp} \). Her results confirmed what has been frequently described for trees, i.e. shoot growth was more affected than root growth (Fig. 1). No significant difference in this sensitivity could be observed among the tested species (\( Q. \) robur, \( Q. \) petraea, \( Q. \) rubra) in neither of these studies.

Data on drought effects on root growth are even scarcer. Root elongation, new root formation and biomass accumulation tend to be very sensitive to soil water depletion. In fact Teskey and Hinckley (1981) demonstrated that the optimal conditions for root growth were at \( \Psi_{wp} \) around -0.5 MPa, and that major decreases occurred even above -1.0 MPa. Nevertheless, they observed continuous slow root elongation at lower \( \Psi_{wp} \).

Control of growth during periods of water shortage may be related to tissue water relations, due to the relationship that exists between cell enlargement, turger and wall extensibility (Cosgrove, 1986). Cellular and tissular water relations are best described using a Föhrler diagram which relates turger (\( P \)), water potential (\( \Psi_w \)) and osmotic potential (\( \pi \)) to the water content. A few assumptions (constant solute content of cells, reflection coefficient of plasmalemma almost equal to one) are necessary. These concepts may be extended from cell to tissue (Tyree and Jarvis, 1982) and data may be obtained using the well known "pressure-volume analysis". The main parameters of interest for ecophysiologists are the osmotic potential at full turger (\( \Psi_{wp} \)), the water potential at turger loss (\( \Psi_{wp} \)), and to a lesser extent, the elasticity coefficient of cell walls.
Fig. 1 - Effects of three levels of soil water potential on shoot and root growth of potted seedlings from 3 species (Q. robur, Q. petraea, and Q. rubra). Values of predawn leaf water potential obtained at the end of a 3 months period are indicated on the x-axis. Shoot and root biomass, and shoot/root ratio are reported. After Scudder (unpub.).

Many descriptions of tissue water relations have been published for oak species (Abrams, 1988; Dreyer et al., 1990). Some examples are listed in table 1. \( \pi_w \) is strongly variable among and within species, as a result of environmental constraints. In general, the most drought tolerant species have a significantly lower \( \pi_w \) and a lower \( \Psi_{wd} \) than susceptible ones, but this is not a general rule.

<table>
<thead>
<tr>
<th>Species</th>
<th>section</th>
<th>( \pi_0 )</th>
<th>( \Psi_{wd} )</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Q. ilex</td>
<td>iles</td>
<td>-1.82</td>
<td>-2.39</td>
<td>young</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-2.43</td>
<td>-4.10</td>
<td>old</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Dreyer et al., 1990</td>
</tr>
<tr>
<td>Q. pubescens</td>
<td>robur</td>
<td>-2.50</td>
<td>-4.00</td>
<td>stand</td>
</tr>
<tr>
<td>Q. alba</td>
<td>iles</td>
<td>-1.47</td>
<td>-2.02</td>
<td>dry</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-1.95</td>
<td>-2.53</td>
<td>Dreyer et al., 1990</td>
</tr>
<tr>
<td>Q. petraea</td>
<td>robur</td>
<td>-1.26</td>
<td>-3.04</td>
<td>greenh.</td>
</tr>
<tr>
<td>Q. rubra</td>
<td>iles</td>
<td>-1.19</td>
<td>-2.67</td>
<td>dry</td>
</tr>
<tr>
<td>Q. alba</td>
<td>iles</td>
<td>-1.47</td>
<td>-2.02</td>
<td>greenh.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-1.95</td>
<td>-2.53</td>
<td>Dreyer et al., 1990</td>
</tr>
<tr>
<td>Q. rubra</td>
<td>iles</td>
<td>-1.19</td>
<td>-2.67</td>
<td>greenh.</td>
</tr>
<tr>
<td>Q. rubra</td>
<td>iles</td>
<td>-1.47</td>
<td>-2.02</td>
<td>greenh.</td>
</tr>
<tr>
<td>Q. elliptica</td>
<td>robur</td>
<td>-0.83</td>
<td>-0.99</td>
<td>May</td>
</tr>
<tr>
<td>Q. elliptica</td>
<td>iles</td>
<td>-1.20</td>
<td>-1.72</td>
<td>July</td>
</tr>
</tbody>
</table>

The most important feature of the tissue water relations lies in the intraspecific variability of all tested parameters. Many factors have been suggested to be able to decrease \( \pi_w \) which enables the maintenance of higher turgor at any given \( \Psi_w \). Light regime during
growth, temperature, mineral nutrition, ontogenetic changes in tissue properties during ageing play probably major roles in affecting \( \pi_p \) as shown by the large differences detected between greenhouse grown and outdoor planted oaks (Dreyer et al., 1990). Periods of drought may also induce an active accumulation of solutes, which could help to maintain significant growth at low water potential. Many data, as summarised by Abrams (1990) showed significant differences in \( \pi_p \) before and after a period of drought. Such differences ranged from -1.3 MPa to -0.3 MPa. It is not clear if these large changes in \( \pi_p \) were solely a response to drought. Some discrepancies probably were due to technical problems during rehydration prior to the measurements of "pressure-volume curves" (Dreyer et al., 1990; Kubiske and Abrams, 1991) and render some of the largest differences questionable. It seems more likely that oaks are able to shift \( \pi_p \) in response to drought by about 0.3 to 0.5 MPa (Osonubi and Davies, 1978, with Q. robur). Parker and Poulard (1988) obtained shifts in \( \pi_p \) of about 0.32, 0.45 and 0.61 MPa for potted seedlings of Q. stellata, Q. alba and Q. macrocarpa respectively. Some authors suspected also that water stress could induce a change in cell wall elasticity (Parker and Poulard, 1988), but these assumptions are often based on "pressure volume" analyses with strong rehydration effects. These data have mainly been obtained for fully expanded leaves. Results for roots are rare (Parker and Poulard, 1988); and no results are available about potential osmoregulation in the growing apices, in particular for root tips. A better knowledge of the water stress effect on root turor, and water relations would be of major importance.

**Water transport from soil to leaves**

Oaks present many particular features in respect to their water transport system. One of the most important lies probably in the large dimension of their rooting system, enabling them to withdraw water from deep soil layers which are generally poorly explored by co-occurring species. Direct observations of 4.5 m deep rooting were reported for Q. alba (Teskey and Hinckley, 1981). In general, rooting of different oak trees remains more superficial, but is always deeper than that of co-occurring species (Hinckley et al., 1981; Abrams, 1990). In situ measurements show a rather deep rooting for 30 year-old Q. petraea (Fig. 2), which roots have grown through a layer of compact clay, and reached depths below 1.80 m. As a result, soil water absorption during a period of imposed water shortage occurred

![Fig. 2 - Rooting profile of 35 yrs old Q. petraea in a stand near Nancy. Percent of root numbers in each soil layer are presented. Deep rooting was observed, despite the presence of a dense clay layer (dark). Observations were stopped at -1.45 m, but soil dehydration profiles revealed even deeper rooting (til -3 m). The line represents the soil water potential profile as measured with psychrometers. It is interesting to observe that the predawn leaf water potential measured during this day matched with the soil water potential of the deepest layers. Data from Brédé (unpub.).](image-url)
summer drought (Guillaumet et al., 1985). A general trend in this respect was also detected by Oosterhuis and Nabuurs (1991) and invoked to explain the occurrence of oak decline in the Netherlands.

Efficiency of the water transport from soil to leaves may be quantitated using the concept of specific hydraulic conductance, either computed on a leaf area basis (Thompson and Hinckley, 1977; Reich and Hinckley, 1989) or on a sapwood area basis (Granier et al., 1989; Bröda et al., 1993). This parameter is directly derived from equation 3, and is often determined using the slope of the diurnal relationship between transpiration and leaf water potential. Reported values observed on mature trees of different species show that, despite large differences in their xylem structure, and their hydraulic architecture, all species display rather similar $g_{s}$ under optimal water supply (Granier et al., 1989). For oak trees, values reported were very similar and independent of tree dimensions and species (Tab. 2). This fact may reveal the maintenance of a balance between potential transpiration (i.e. leaf area) and absorption (root area).

Table 2 - Optimal values of soil to leaf specific hydraulic conductance ($g_{s}$) of different species of oaks under well watered conditions. Estimates using the predawn leaf water potential as an index of soil water potential, and values of transpiration obtained either with xylem sap flow monitoring, with weighing techniques or with measures of leaf transpiration.

<table>
<thead>
<tr>
<th>Species</th>
<th>$g_{s}$</th>
<th>Material</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mmol m${}^{-2}$ s${}^{-1}$ MPa${}^{-1}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Q. robur</td>
<td>1.4</td>
<td>Adult tree</td>
<td>Cermak et al., 1980</td>
</tr>
<tr>
<td></td>
<td>1.1</td>
<td>Potted seedlings</td>
<td>Simons et al., 1993</td>
</tr>
<tr>
<td>Q. petraea</td>
<td>1.2</td>
<td>Adult tree</td>
<td>Bröda et al., 1993</td>
</tr>
<tr>
<td>Q. rubra</td>
<td>1.8</td>
<td>Pygmy trees</td>
<td>Reich and Hinckley, 1989</td>
</tr>
<tr>
<td>Q. marilandica</td>
<td>1.5</td>
<td>Pygmy trees</td>
<td>Reich and Hinckley, 1989</td>
</tr>
<tr>
<td>Q. alba</td>
<td>1.0</td>
<td>Adult tree</td>
<td>Thompson and Hinckley, 1977</td>
</tr>
</tbody>
</table>

The leaf-specific hydraulic conductance $g_{s}$ is strongly affected by drought and decreases more or less steeply with decreasing predawn water potential in all trees that have been studied. Bröda et al. (1993) showed in a field study that for Q. petraea trees the relationship to $\Psi_{wp}$ displayed a steep decrease at $\Psi_{wp}$ above -1.0 MPa, followed by a period of gradual decline (Fig. 3). The same observation was made on Q. robur seedlings, where $g_{s}$ initially decreased sharply from 1.0 to less than 0.5 mmol m${}^{-2}$ s${}^{-1}$ MPa${}^{-1}$ between -0.2 and -1.2 MPa $\Psi_{wp}$ but remained rather constant thereafter (Simons et al., 1993). Other reported reactions to drought displayed also the first phase of decline; but the limited decrease in $\Psi_{wp}$ did not allow any conclusion to be made for the second phase (Fig. 3, Thompson and Hinckley, 1977 Q. alba, Reich and Hinckley, 1989 Q. marilandica and Q. rubra).

![Graph](image-url)

**Fig. 3** - Drought induced decline in the soil-to-leaf specific hydraulic conductance ($g_{s}$) from different oak species under different experimental conditions. A good homogeneity appeared under high predawn water potentials, independently of experimental design, tree dimensions and species. Drought induced decline was slightly different among species. Data from Bröda et al. (1993, adult trees of Q. petraea), Simons et al. (1993, potted saplings of Q. robur), Thompson and Hinckley (1977, adult Q. alba) and Reich and Hinckley (1989, pygmy trees of Q. rubra and Q. marilandica).

The steepness of the decline in $g_{s}$ with decreasing $\Psi_{wp}$ appeared also very variable with species. In conifers for instance, $g_{s}$
was shown to decline much more rapidly than in oaks (Granier and Colin, 1990). The oak species grouped in figure 3 also behaved
differently. Q. rubra seemed much more sensitive than Q.
marilandica in the Reich and Hinckley (1989) study, while Q. robur
and Q. rubra were intermediate. The significance of such differences
remains difficult to assess.

As discussed by Breda et al. (1993) rooting patterns may greatly
influence the relationship between $B_l$ and $W_{x, s}$. The leaf-specific
hydraulic conductance $B_l$ includes a large set of resistances. The
hydraulic resistance of soils increases with decreasing water content;
moreover, the steepness of this increase is dependent on soil
properties, as shown for peat-silt mixtures by Orlandi and Due
(1986). The effective area of the soil-root interface may decrease as
soon as dry soil layers increase. The xylem resistance in roots, trunks
and leaves, may increase due to vessel embolization. Finally, the
resistance from xylem vessels to evaporating areas in the substomatal
chambers may play an important role. The relative contribution of
each of these resistances to the overal tree resistance during drought
is still poorly known, but some new data allow an assessment of
the importance of xylem dysfunction in this respect.

The hydraulic architecture of oaks is well known. Oaks, at least
the tallest, deciduous species, are ring-porous with wide vessels.
Vessel dimensions have been frequently assessed. Diameters of
vessels may be as much as 80 μm in early-wood and 25 μm in late
wood of Q. rubra and Q. alba (Cochard and Tyree, 1990). Vessel
lengths are less frequently described, due to the complicated staining
techniques involved. Cochard and Tyree (1990) showed that a
majority of cells in current year shoots of Q. rubra and Q. alba
vessels were a few cm long, but that current year wood on 2-year
shoots already bore a significant number of vessels above 1 m. A
similar observation was made by Simonin et al. (1993) for seedlings
of Q. robur. Vessels in trunks may be much longer, reaching several
meters (Zimmermann and Brown, 1971). Oak vessels show no
significant spiralling. As a consequence of these high diameters and
low resistances to water flow, sap velocity is very high (till around 20
m h⁻¹, Huber and Schmidt, 1936; Miller et al., 1980). The precise
location of pathways for water flow in trunks and branches is still
under debate. Some authors claim that circulation of water is
restricted to the very last year ring; they base this assumption on the
observation that hydraulic conductivity of twigs declines till almost
nil after the first frost during Autumn (Cochard and Tyree, 1990). On
the other hand, direct measurements using sap flow monitoring
techniques (either Heat Pulse techniques, or constant heated
electrodes) showed that although the main flux was concentrated in
the external year ring, there is still some flow in the next few mm
(which is about 3-4 year rings) (Miller et al., 1980; Cermak et al.,
1992; Breda et al., 1993). The nature of water conducting vessels in
older year-rings is not clear; associated short vessels and late wood
vessels may participate strongly. In fact, experiments in which the
external ring was severed revealed that the total flux a few dm above
the severing could be maintained at an almost constant rate (Granier,
unpub.). A definitive conclusion is therefore still not possible, but it
appears highly probable that, despite the strong freeze-thaw
embolization which may happen during winter in large vessels, at
least 2-4 supplemental year rings participate to the total flux in stems
of oak trees.

A main point of discussion on the hydraulic architecture of oaks
has been the extent to which these large vessels with low resistance
were safe and not prone to cavitation. Mechanisms for drought
induced cavitation have been studied extensively (Tyree and Spery,
1988; Cochard et al., 1992b). The cause may be the passage of air
bubbles from empty vessels into vessels under tension. The tension
which may be sustained by an air-water interface in the pit-
membranes yields the threshold for cavitation in this vessel. Vulnerability curves may be determined by relating the leaf water
potential attained to the relative loss of conductivity in the branches.
Different techniques have been developed for such studies (bench
dehydration, pressurisation, dehydration of seedlings in situ) and yield
very similar results (Cochard et al., 1992b; Tyree et al., 1992;
Simonin et al., 1993). Vulnerability curves have already been
established for some different oak species and yielded very interesting
results (Cochard and Tyree, 1990; Cochard et al., 1992a; Simonin et
al., 1993): (1) no losses of conductivity were detected before rather
low values of water potential (around -1.8 MPa in the most vulnerable
species, which was Q. rubra and around -2.5 in Q. petraea and Q.
pubescent; (2) after the initial threshold there was a steep increase in
the loss of conductivity, leading to almost 100% loss of conductivity
after an additional decrease of 1 to 1.5 MPa depending on the species;
(3) very consistent interspecific differences could be detected. In
general, Q. rubra appeared as the most vulnerable among tested
species, followed by Q. robur, Q. petraea and Q. pubescent (Cochard
et al., 1992a ). Comparisons with other species revealed that these
degrees of vulnerability were much lower than those detected in pioneer species (Juglans regia, Cochard et al., 1992b; Populus deltoides, Tyree et al., 1992), and in many tropical species like Schefflera morototoni (Tyree et al., 1991) but higher than in probably present a diffuse porous structure, and have still to be tested Rhizophora mangle (Tyree and Ewers, 1991) or drought adaptation for their susceptibility to cavitation and embolism.

Transpiration and stomatal regulation

Stomatal regulation of water loss by leaves plays probably a major role in the responses of trees to drought, as stomata constitute the most tightly regulated conductance in the pathway from soils to the atmosphere. Our understanding of stomatal function has been greatly improved in the last decade, although some uncertainties remain about the precise role of stomatal control at a whole tree level, and the identity of physiological processes governing stomatal behaviour during drought.

Stomata of oak trees do of course close when soil water is depleted. This fact is nicely illustrated by the figure 4 (Bréda et al., in prep.) which shows the relationship between drought (measured as the predawn leaf water potential) and the stomatal conductance measured on sun exposed leaves at noon. This relation shows a clear decline at a high water potential, followed by a slower decline at lower water potentials. Similar responses were commonly displayed by potted saplings of almost all tested oak species (Eppron and Dreyer, 1990; Eppron et al., 1995; Vivion et al., 1993). During measurements under natural conditions, values at noon may be much lower than those during early morning: in fact, diurnal cycles of $g_w$ tend to display marked variations with frequent midday depressions in $g_w$, especially in sclerophyllous oaks under dry conditions (Temeles et al., 1985), but also in mesic species like Q. robur or Q. rubra during bright and warm days even in the absence of any decrease in predawn water potential (Eppron et al., 1992). Drought eventually amplifies this midday depression. Midday depression has been ascribed to direct responses of stomata to increasing leaf to air vapour pressure differences ($\Delta w$), but the mechanism by which these changes in $\Delta w$ are sensed is still a matter of debate.

Decreases in leaf water potential have long been supposed to be the trigger mechanism for stomatal closure, but many studies on different woody and herbaceous species have revealed that stomatal closure may be independent of actual leaf water potential. Experiments with pressurised roots, or with root systems split into...
two compartments with different watering regimes, have shown that some kind of signal could be transported to shoots independently from water potential and induce stomatal closure (Davies and Zhang, 1991). There have been few relevant studies on oaks. Dreyer and other species, the content in abscisic acid of xylem sap extracted from roots or from leaves increased significantly during drought, for all the species they tested, with no significant differences with many other

species. The precise role of root sourced ABA in the induction of stomatal closure remains to be assessed.

For the range of oak species tested, differences in the response of $g_w$ to drought induced decline in $\Psi_w$ are small. During all experiments during which different species were submitted to drought in parallel, the decline in $g_w$ was almost of the same magnitude and precocity. This has been observed by Scuiller (1990) with 5 different species of the robur section (Q. robur, Q. petraea, Q. pubescence, Q. pyrenaica, Q. canariensis). The same observation applies to a direct comparison of Q. petraea and Q. robur in a stand (Bréda et al., in prep.), to comparisons among young trees of Q. petraea, Q. robur and Q. rubra (Vivin et al., 1993), or among potted seedlings of Q. petraea, Q. cerris and Q. rubra (Epron et al., 1993). This observation may lead to the question whether interspecific differences in stomatal reactions play a significant role in the adaptation of species to drought. Moreover, in the case of the studied oak species, there was no correlation between susceptibility to cavitation and precocity of stomatal closure with increasing water stress; despite large differences in vulnerability to cavitation, Q. robur, Q. petraea, Q. robur, Q. cerris, Q. pubescence displayed similar responses to decreasing predawn leaf water potential (Figs. 4 and 5). In contrast, strong correlations have been observed between the decrease in $g_w$ and stomatal conductance in coniferous trees (Lu and Granier, pera, com.). This point clearly deserves further research.

Photosynthesis

Stomatal closure is known to reduce diffusion of $CO_2$ to chlorophyll and therefore limit the rates of net $CO_2$ assimilation. The responses of photosynthesis to drought have been addressed in numerous studies, but it is worth notice that the potential rates of net $CO_2$ assimilation of oak leaves are probably much greater than sometimes reported (Ceulemans and Saugier, 1991). Some of the highest reported values are summarized for different species in table 3; they were above 12 $\mu$mol m$^{-2}$ s$^{-1}$ in many cases and we observed values near 25 $\mu$mol m$^{-2}$ s$^{-1}$ in a Q. cerris coppice of central Italy. Such values may not be reached under all conditions, but demonstrate that many oak trees, including sclerophyllous evergreens, have nevertheless high photosynthetic potentials. In comparison with cultivated crops, these rates are still rather low. $CO_2$ saturated photosynthesis is much higher, and the few available reports yield values around 25 to 30 $\mu$mol m$^{-2}$ s$^{-1}$ under 5% $CO_2$ (Tab. 3). One of
Table 3 - Maximal net CO₂ assimilation rates measured on different oak species: (a) under ambient CO₂ (<35 Pa) and saturating irradiance; (b) under saturating CO₂ and irradiance.

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>Net assimilation (µmol m⁻² s⁻¹)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Q. robur</td>
<td>seedlings</td>
<td>16-17</td>
<td>Vivin et al., 1993</td>
</tr>
<tr>
<td>Q. petraea</td>
<td>seedlings</td>
<td>17</td>
<td>Vivin et al., 1993</td>
</tr>
<tr>
<td></td>
<td>adults</td>
<td>14-15</td>
<td>Epron et al., 1992</td>
</tr>
<tr>
<td>Q. rubra</td>
<td>seedlings</td>
<td>12-13</td>
<td>Vivin et al., 1993</td>
</tr>
<tr>
<td></td>
<td>seedlings</td>
<td>11-12</td>
<td>Weber and Gates, 1990</td>
</tr>
<tr>
<td></td>
<td>coppice</td>
<td>10</td>
<td>Briggs et al., 1996</td>
</tr>
<tr>
<td>Q. alba</td>
<td>adult</td>
<td>9</td>
<td>Dougherty and Hinckley, 1981</td>
</tr>
<tr>
<td>Q. ellipposialis</td>
<td>adult</td>
<td>Wisconsin</td>
<td>13</td>
</tr>
<tr>
<td>Q. coccifera</td>
<td>shrub</td>
<td>Portugal</td>
<td>8.9</td>
</tr>
<tr>
<td>Q. robur</td>
<td>shrub</td>
<td>15</td>
<td>Tenhunen et al., 1987</td>
</tr>
<tr>
<td>Q. petraea</td>
<td>seedlings</td>
<td>5% CO₂</td>
<td>30</td>
</tr>
<tr>
<td>Q. coccifera</td>
<td>shrub</td>
<td>0.5% CO₂</td>
<td>25-30</td>
</tr>
</tbody>
</table>

The factors limiting net CO₂ assimilation rates may be the low mesophyll conductance to CO₂ (gₘ, that is the high resistance to the diffusion from intercellular spaces to the chloroplast stroma) as measured by oaks together with many other tree species. Recent determinations with techniques based on natural discrimination from photochemical efficiency of PS II, showed that gₘ was below 0.150 mol m⁻² s⁻¹ in Q. rubra and in Q. ilex as compared to 0.690 for wheat (Di Marco et al., 1991; Loreto et al., 1992). Such values are of the same order of magnitude as stomatal conductance and may therefore strongly contribute to the limitation of diffusion of CO₂ to chloroplasts and as a consequence net assimilation rates. A thorough comparison of oak species with their variable three-dimensional leaf structures would be useful.

Water stress induced declines in A are parallel to those in gₘ (Fig. 5). An analysis of diurnal cycles of A revealed that during the first hours in the morning oaks were still able to photosynthesize at highly significant rates even under very severe stress conditions. Epron et al. (1992) for instance observed rates of about 40% of controls on Q. petraea trees with Vₚₚ around -2 MPa. An analogous observation was made for severely stressed trees under mild weather conditions, that is low VPD and irradiance. This observation leads to three remarks. (1) The response of oak photosynthesis to water stress appears to be rather gradual, and is modulated by microclimatic factors including VPD, irradiance and leaf temperature. The ability of oaks to maintain significant values of A had already been highlighted by Dougherty and Hinckley (1981) with Q. alba. (2) The primary effect of drought seems to be to enhance the midday depression in A, as shown by many authors for different species as Q. coccifera (Tenhunen et al., 1985). (3) The establishment of drought response curves for A may yield very diverse results depending on the actual conditions during measurements.

A direct comparison of species may therefore be misleading if care is not taken to use similar conditions, but it is also necessary to make comparisons under a range of differing microclimates. Under limiting light conditions, Q. petraea, Q. rubra and Q. cerasus tended to have the same rates of decline (Epron et al., 1993). Similarly, Vivin et al. (1993) found no significant differences between Q. petraea, Q. robur and Q. rubra under a transparent roof. Ni and Pallardy (1991) observed a better maintenance of A in Q. stellata than in Q. alba with decreasing leaf water potential. Adequate assessment of species-related differences is rather difficult due to the lack of data.

The physiological mechanisms of the action of drought on photosynthesis are still a matter of debate for oaks as well as for many other plant species. Some authors have claimed that the limitation of A could not be ascribed to the stomatal closure alone, as calculated values of intercellular CO₂ concentration (cₜ) remain often high during stress (Briggs et al., 1986). Others have observed that drought induced stomatal closure occurred non-uniformly, so that cₜ
Fig. 5 - Drought induced decline of stomatal conductance to water vapour ($g_w$) and net CO$_2$ assimilation rate ($A$) observed with potted seedlings from five species of oaks in a climate chamber. No clear differences could be detected in the differences in $g_w$ and $A$ on control plants (represented as mean ± standard deviations).

calculation could be misleading. Occurrence of "stomatal patchiness" during water stress on oak leaves has been studied by a few authors using $^{14}$CO$_2$ labelling (Ni and Pallardy, 1992; Epron and Dreyer, 1993). No general trend has been detected, and Epron and Dreyer (1993) concluded that patchiness occurred on oak leaves submitted to drought, but that it was not related to the heterobasic anatomy of the leaves, and that it probably could not explain the discrepancy between high values of calculated $c_i$ and the maintenance of high potential photosynthesis. Other arguments have been developed to demonstrate that water stress effects on photosynthesis were mainly mediated by stomata. (1) The photochemistry of oak leaves appears to be rather insensitive to leaf dehydration in the dark, and relative water content (RWC) needs to be decreased below 0.3 before the first damages to PS II can be detected (Epron and Dreyer, 1992). On the same leaves, the first signs of dysfunctions after 10 min of induction at a PFD of 220 $\mu$mol m$^{-2}$ s$^{-1}$ were observed at a RWC below 0.75, that is largely below the turgor loss point. (2) When potted saplings were submitted to a gradual dehydration under moderate irradiance (400 $\mu$mol m$^{-2}$ s$^{-1}$), A declined but $A_{max}$ measured under saturating irradiance and 5% CO$_2$ was maintained at almost constant rates, together with the electron flow rate through PS II (Fig. 6, Epron and Dreyer, 1993). Stomatal closure seems therefore to be the main factor limiting rates of net CO$_2$ assimilation during drought in oaks as well as in other species.

The above results were obtained under low irradiance and with relatively short periods of drought. Under natural conditions however, leaves exhibiting low assimilation rates due to stomatal closure may be exposed to additional stresses as high irradiance and high temperature, which may be of consequence to the photosynthetic activity. To explore this possibility, Epron et al., 1992 and Epron and Dreyer (in prep.) analysed the photochemical efficiency of PS II of dark adapted leaves of Q. petraea and Q. robur and followed (1) diurnal cycles on severely stressed trees, (2) seasonal evolution of its predawn value before, during and after a period of drought. Diurnal cycles showed clear decreases in this efficiency, which were steepest in droughted trees but could also be detected in controls as soon as net CO$_2$ assimilation was light saturated. But these decreases were completely reversible and as a consequence, no long term effect could be detected. The observed decreases had therefore to be interpreted not as a degradation process (i.e. photoinhibition), but as a down regulation of its photochemical activity (that is its quantum yield and
rate of electron production) to match decreased need for photosynthetic reducing power. The mechanism by which this down regulation may be achieved is under discussion, but in all cases it implies an increase in the thermal dissipation of excess excitation energy by PS II chlorophyll antennae. This view may be strengthened by the observation that after very few hours of relaxation under semidarkness, these changes were completely reversed and PS II efficiency again optimal. Even under the strongest drought we never observed long term degradation of PS II. Measurements of actual photochemical efficiency of PS II in vivo on Q. cerris (Valentini et al., in prep.) and on Q. robur (Epron, 1993) displayed very rapid diurnal fluctuations in response to changes in irradiance.

The above observations were achieved with stressed trees still displaying significant rates of net assimilation. But with potted saplings of Q. petrea, Q. rubra and Q. cerris, more severe stress ($\Psi_{wp} = -3$ MPa) associated with moderate irradiance drove to stronger effects: an exposure to high irradiance led to greater decreases in the photochemical efficiency measured after 90 min relaxation in leaves of stressed vs. controls, with the exception of Q. cerris, which seemed to display a slightly more efficient protection that the two other species (Epron et al., 1993).

Oak trees, even the mesophytic species, seem therefore able to maintain the integrity of their photosynthetic apparatus during periods of severe stresses. As a consequence, oak leaves maintain a good ability to fully recover high photosynthetic rates after rehydration following a drought. But effects of combination of drought with high temperatures still have to be tested. High leaf temperatures, that is above 35 to 40 °C may have deleterious effects as they do in many other species. This factor could play a major ecological role as it is often associated with drought under semi-arid conditions. The ability to recover from high temperature stresses, and potential interspecific differences among oak species still have to be tested and the precise physiological basis of the protection mechanisms acting during stress remain to be precisely understood.

**General conclusion**

Different responses of trees to periods of drought have been defined by ecologists. In general, desiccation tolerance is opposed to desiccation avoidance. Trees adopting the former behaviour cope with desiccation and keep their stomata significantly open even with low water availability while in the latter case, trees close their stomata early.

Oak trees display the first behaviour. The main features allowing this conclusion are summarised in table 4. A general functional model may be derived from these observations. Low susceptibility to cavitation and deep rooting ability appear as central features in this model. These adaptations allow high rates of transpiration even after
Table 4 - Main eco-physiological features associated with the two strategies displayed by trees in front of soil water depletion. Oaks display mainly features associated with the tolerance strategy.

<table>
<thead>
<tr>
<th>Feature</th>
<th>Avoidance strategy</th>
<th>Tolerance strategy</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Vulnerability to drought induced embolism</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2. Rooting pattern</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Hydraulic segmentation</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Leaf water potential (midday)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Stomatal closure</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Transpiration during drought</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Leaf temperatures</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- CO₂ assimilation</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Risk of photoinhibition</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3. Growth under limited water supply</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Osmoligilation</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4. Growth under optimal water supply</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Ecological behaviour</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

relatively long periods of water shortage. Low values of water potential may be reached in leaves, with only limited embolization of vessels, and with no consequence for photosynthesis. Stomata remain open till very low water potentials, allowing maintenance of significant net CO₂ assimilation rates and contributing to a prevention of overheating and photoinhibitory damage.

These features seem to be relatively general in the mesophytic species of the genus Quercus. Data are still too scarce to define a particular feature of this genus as compared with other mesophytic species rather than pioners. The particular behaviour of late successional xerophytic and evergreen species like Q. ilex and Q. suber, which display a diffuse porous wood anatomy, and very particular leaf structure, is probably somewhat different from the general frame presented here. But data for these species remain rare. There is still a vast domain for further research in the connections between physiological traits of tree species and their ecological consequences.

ACKNOWLEDGEMENTS

Many of the described studies have been made at Nancy in the frame of an EEC project (STEP CT 90 0050C: "Water stress, xylem dysfunction and dietetic mechanisms in European Oak Trees"). The authors wish to thank H. G. Jones and M. T. Tyre for helpful comments on this manuscript.

For correspondence and reprints contact E. Dreyer.

REFERENCES


For., 42: 1-22.


SCUILLER L., 1990. Exploration de la variabilité des comportements écophysiologiques de semis de chênes blancs européens soumis à la sécheresse. These Doctorat, Université de Nancy I, 103 pp.


