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Differences in drought resistance among 3 deciduous oak species grown in large boxes

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Summary — The purpose of this study was to explain large differences in growth and decline of the pedunculate oak (*Quercus robur* L) and the sessile oak (*Q petraea* Liebl) observed in the forest as a result of drought. In addition, northern red oak (*Q rubra* L) was compared with the 2 indigenous oaks. The effects of controlled soil water deficits on growth and water relations of young plants of these 3 species grown in large boxes have been studied. The plants were old enough to have developed normal root systems. Two species were planted in each box, and submitted to very similar patterns of water stress. Predawn leaf water potential, stomatal conductance, net assimilation rates, shoot elongation and mortality were monitored. The effect of an overall improvement in mineral nutrition on these parameters was also tested. During water deficit (decrease in predawn leaf water potential), the pattern of decrease of gas exchange was similar for the 3 species. Thus, their ability to limit water deficit by reduction of transpiration was similar. On the other hand, shoot growth of *Q rubra* was more reduced than that of *Q robur* for similar predawn leaf water potential; growth of *Q petraea* was the least sensitive. However, increase of mineral nutrition improved the growth of both *Q robur* and *Q rubra*, but not that of *Q petraea.* For the 3 species, no mortality was noted as long as predawn leaf water potentials remained > –3.6 MPa. Below this limit, the mortality rate was highest in *Q robur*, *Q petraea* and lowest in *Q rubra*. These differences in mortality between species are due to differences in tolerance to water stress, not in avoidance.

drought / growth / gas exchange / dieback / fertilization / *Quercus*

Résumé — Différences dans la résistance à la sécheresse de 3 espèces de chêne à feuilles caduques, cultivées en conteneurs. *Le but de ce travail était d'expliquer les grandes différences de croissance et de dépérissement observées en forêt suite à des sécheresses, entre le chêne pédonculé (*Quercus robur *L) et le chêne sessile (*Q petraea *Liebl). De plus, le chêne rouge d'Amérique (*Q rubra *L) a été comparé aux 2 chênes indigènes. Les effets d'un déficit hydrique édaphique contrôlé sur la croissance et les relations hydriques de jeunes plants de ces 3 espèces, cultivés dans de grandes cuves, ont été étudiés. Les plants étaient assez âgés pour avoir pu développer des systèmes racinaires normaux. Deux espèces ont été plantées dans chaque cuve, subissant ainsi* *exactement à chaque moment le même stress hydrique. Les variables suivantes ont été prises en compte : potentiel hydrique foliaire de base, conductance stomatique, assimilation nette, croissance aérienne et mortalité. L'effet d'une amélioration globale de la nutrition minérale sur ces paramètres a été également étudié. En situation de déficit hydrique (diminution du potentiel hydrique de base), le modèle de diminution des échanges gazeux a été similaire pour les 3 espèces; ainsi, la manière dont elles évitent le stress hydrique est quasiment identique. En revanche, la croissance aérienne de* Q rubra *a été plus réduite que celle de* Q robur *pour un même potentiel hydrique foliaire de base, la croissance de* Q petraea *était la moins sensible. Cependant, une amélioration de la nutrition minérale a augmenté la croissance de Q rubra et Q robur, mais non celle de* Q petraea. *Pour les 3 espèces, aucune mortalité n'a été notée pour des potentiels hydriques de base > –3.6 MPa. En dessous de cette limite, pour les plants ayant subi des conditions similaires, les taux de mortalité furent plus élevés chez* Q robur *que chez* Q petraea, *et très faibles chez* Q rubra. *Ces différences de mortalité entre les espèces semblent dues à des différences de tolérance et non à l'évitement au stress hydrique.*

sécheresse / croissance / échanges gazeux / mortalité / fertilisation / **Quercus**

INTRODUCTION

After a severe drought in 1976, oak decline occurred in several regions of France (Centre, Bourgogne, Pyrénées Atlantiques). This phenomenon was of concern on account of its intensity and economic consequences. Similar decline in oaks was also observed both in Europe (Delatour, 1983; Osterbaan and Nabuurs, 1991) and in the USA (Tainter *et al,* 1983; Abrams, 1990).

Initial phytoecological studies carried out in different regions (Becker and Levy, 1982; Durand *et al,* 1983; Macaire, 1984) revealed that only the pedunculate oak (*Quercus robur* L) was subjected to decline whereas the sessile oak (*Quercus petraea* Liebl) remained unaffected. Soil water deficit appeared to be the determining factor (Becker and Levy, 1983); other factors such as mineral nutrition, pathogenic agents and forestry must be considered as only secondary and exacerbating. Furthermore, other studies (Becker and Levy, 1990) revealed that both the ecological differences between the 2 species, and the artificial spread (*ie* planting) of *Quercus robur* to unsuitable sites had led to large differences in radial growth in a great number of stands. These differences might to be due to a greater demand by *Q robur* than *Q petraea* for water and to some degree for nutrients. Another troublesome point was that, although morphological characteristics distinguish the 2 species (Dupouey, 1983; Sigaud, 1986), forest managers have made little distinction between the 2 oak species when reestablishing stands. It is therefore not surprising that in many sites *Q robur* does not seem to be suitably located from an ecological point of view.

From an ecophysiological point of view, and with regard to the water relations of these 2 indigenous species, preliminary experiments on seedlings showed that *Q petraea* was better able to avoid both internal water stress and severe soil drought than *Q robur.* Hence, according to Colleu (1983) on the one hand an initiation of more numerous secondary roots furthers root uptake and decreases internal water stress, but produces an increase in soil drought; and on the other hand, a stomatal control which occurs at higher water potential and more effectively reduces water losses and soil drought. However, the differences in behaviour that have been observed in young plants were not as well expressed in forest stands. Moreover, these studies were carried out with seedlings grown in pots with a confined root system development, which considerably limited the practical relevance of the results obtained.

Thus, the purpose of this study was to characterize in a comparative manner the effects of a prolonged soil drought on the ecophysiological functioning of oaks grown outdoors in large boxes, allowing us to work on older plants with a normal root system development. It must be emphasized that this experimental design (*ie* large boxes, binary mixed species) allowed accurate interspecific comparisons for characterization of soil drought intensity. Moreover, it was also interesting to investigate the ecophysiological relations of northern red oak (*Quercus rubra* L) in comparison with the 2 indigenous oaks, and determine the former's drought sensitivity. In fact, *Q rubra* is one of the most remarkable species introduced in Europe for reestablishing stands in unfavorable ecological sites (Timbal, 1990) in particular due to its rapid growth.

MATERIALS AND METHODS

Experimental design

The experimental design was set up near the INRA Research Centre of Nancy (in Lorraine, northeast France). It consisted of 26 large boxes (depth: 100 cm, volume: 1.62 m^3), which were partially buried. These boxes were filled with 10 cm of gravel at the bottom to improve water drainage, and 90 cm of a sandy loam soil from the horizon A_1/A_2 of a brown soil from the Mondon Forest (France) mixed with peat in the upper 10 cm.

In March 1987, 2-yr-old saplings from the Forest Research Centre's nursery were planted (2 species and 40 plants per box). In order to avoid any possible microclimatic effects due to site conditions, the allocation of species in the different boxes was randomized. However, species having the strongest juvenile growth were planted to the north of each box, so as to reduce the competition for light. All trees were grown in open conditions and, during the first few years, developed vigorously, creating closed canopy stands. Some *Q rubra* whose development was too great and detrimental to the other plants had to be pruned.

In May 1990, 2 greenhouses covered with a transparent plastic sheath and largely opened at their extremities were installed to intercept rainfall while maintaining sufficient ventilation, thus avoiding an increase in temperature during hot summer days.

Plant conditioning

The experimental design adopted for each species association was a 3 x 2 factoral design consisting of 3 watering regimes and 2 nutrient availability treatments (see table I).

Water supply regimes

The 3 water supply regimes were as follows:

- control boxes (W) maintained permanently near field capacity by frequent watering (3 x 50 l per week);
- boxes (D) submitted to moderate drought, then brought back to field capacity whenever av-

Table I. Number of boxes per treatment and oak species association.

Box	*Treatment*					
	Wu	*Wf*	*Du*	*Df*	*DDu*	*DDf*
Q robur Q petraea	2	1	2	1	2	1
Q rubra Q robur	2	–	2	1	2	1
Q rubra Q petraea	2	1	2	1	2	1

erage predawn leaf water potential reached –2.0 MPa (each time 2 x 150 l within 2 d);

- boxes (DD) submitted to severe drought up to –4.0 MPa and then brought back to field capacity (2 x 150 l within 2 d).

The water supply in the control treatments represented ≈ 92 l m^{-2} weekly. As a result, irrigation was greater by a factor of ≈ 3 than the observed ETP rate at Nancy and hence could have given rise to nutrient leaching.

Drought in the dry treatments began on May 22 (Julian day 142). From August 30 onwards (jd 242), the boxes at field capacity were no longer watered.

Levels of mineral nutrition

The 2 levels of mineral nutrition were as follows:

- unfertilized boxes (u);
- boxes with a supply of NPK mineral fertilizer (f): 220 g/m^2 patentkali, 160 g/m^2 triple super phosphate and 37 g/m^2 ammonitrate were added manually.

Ecophysiological measurements performed

Water relations

Predawn leaf water potential (ψ_{wp}) was measured using a pressure chamber (Aussenac and Granier, 1978) and was determined before sunrise at least once a week on an average plant per species and per box.

Gas exchange

Net CO_2 assimilation rate (*A*, µmol m^{-2} s^{-1}) and stomatal conductance for water diffusion (g_w, mmol m^{-2} s^{-1}) were performed *in situ* using a portable gas exchange measurement system (Li 6200, Li-Cor, USA) under natural climate and irradiance, and expressed on a leaf area basis using a portable area meter (Li 3000A, Li-Cor, USA). Gas exchange was determined once a week from 11 am to 01 pm when the sun was at its zenith, on the leaf of 1 average plant per species per box. Only leaves exposed to full light were selected.

Shoot elongation and mortality

Shoot elongation measurements were carried out once a week on 10 plants per species per box. In order to determine whether a part of the difference in *Quercus* drought behaviour was due to a difference in tolerance to low water potentials, all the boxes were subjected to extreme drought conditions by withholding irrigation after August 30 (jd 242). When ψ_{wp} reached –5.0 MPa, the soil was watered to field capacity in order to estimate the survival rate of each species. Mortality rate was assessed the following year on June 10 1991 (jd 160) in all treatments.

RESULTS

Predawn leaf water potential

As illustrated in figure 1, the time course of predawn leaf water potential (ψ_{wp}) was virtually identical for each couple of species grown in a given box up to the lowest values of ψ_{wp} (–4.0 MPa). This results implied that there was no interspecific heterogeneity in the exploitation of the soil water with the possible exception of some fertilized treatments submitted to drought (see fig 1, upper right).

Under controlled conditions, ψ_{wp} ranged from –0.05 to –0.60 MPa for all species; the fluctuations were mainly dependent on delays in recovery of field capacity.

For the moderately dry treatments, ψ_{wp} reached –2.0 to –3.0 MPa depending on the boxes. Two rehydrations to field capacity were carried out according to the experimental design (jd 183, jd 203). The first drought period lasted 41 d while the second was shorter (23 d).

Concerning the severely dry treatments, the decrease of ψ_{wp} was also rapid: 64 d, to reach –4.0 MPa on average. Consequently, irrigation to field capacity (jd 207) was essential in order to prevent the plants from early wilting. Then plants were sub-

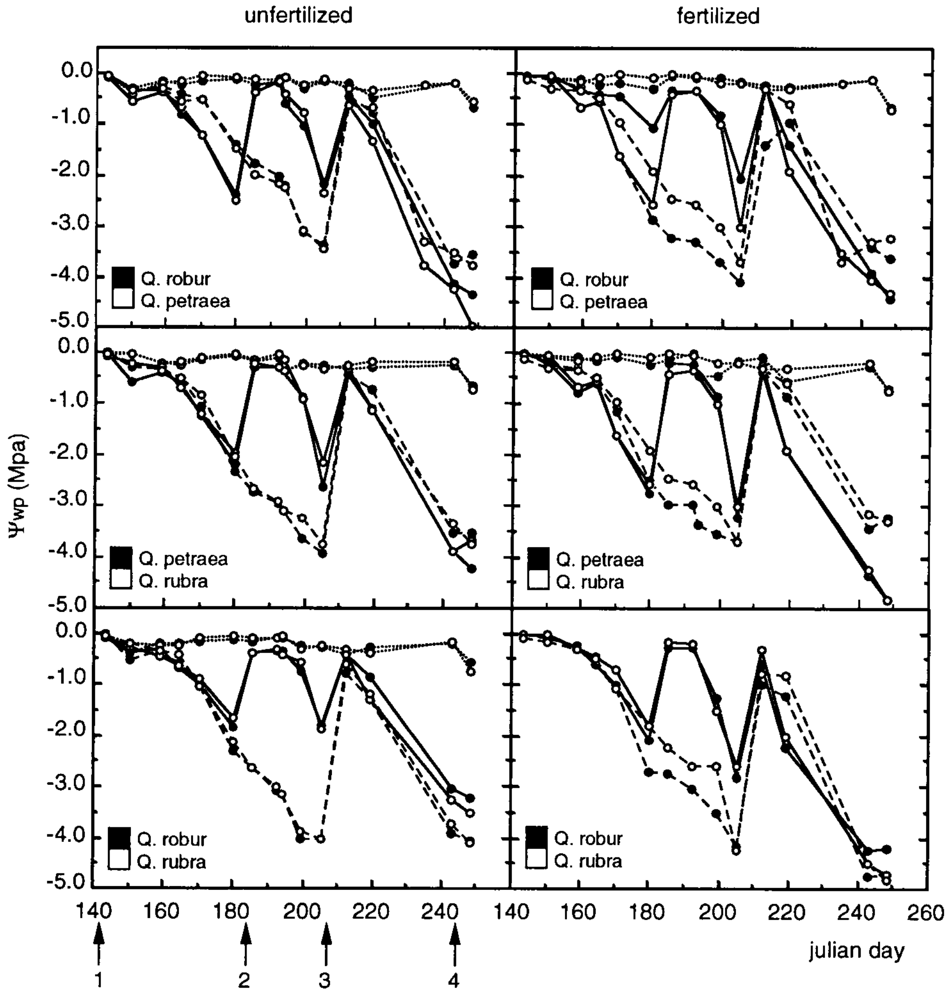

Fig 1. Evolution of predawn leaf water potential (ψ_{wp}, MPa) in relation to Julian days for 3 species associations and 2 nutrition levels. Dotted line, solid line and dashed line represented W, D and DD water treatments respectively; full and open symbols represented the 2 species in each graph. The 4 arrows indicate: 1) onset of drought; 2) or 3) field capacity rewatering for D and DD treatments; 4) onset of final drought for all treatments (see Materials and Methods for more details).

mitted to very severe water deficits (–5.0 MPa). In this case, predawn leaf water potential decreased rapidly (in 2 od it again reached –4.0 MPa).

These kinetics revealed differences in the evolution of the soil drought according to treatments. As far as fertilization was concerned, one can only assume that because of a greater biomass in the fertilized boxes (especially in controlled conditions) the total transpiration was higher and induced faster soil water depletion.

Net photosynthesis and stomatal conductance

Evolution of CO_2 assimilation rates *(A)* and stomatal conductance for water (g_w) with respect to predawn leaf water potential (ψ_{wp}) is displayed in figure 2. Each point represents a measurement performed on a sunny day from 11 am to 01 pm on an average plant per species per box. Values corresponding to PPFD < 800 μmol m^{-2} s^{-1} or to recent rehydration were not plotted.

When ψ_{wp} was not limiting ($\psi_{wp} > -0.75$ MPa), the stomatal conductance and photosynthesis values showed wide variability. This heterogeneity could be explained by a wide intraspecific variability (choice of

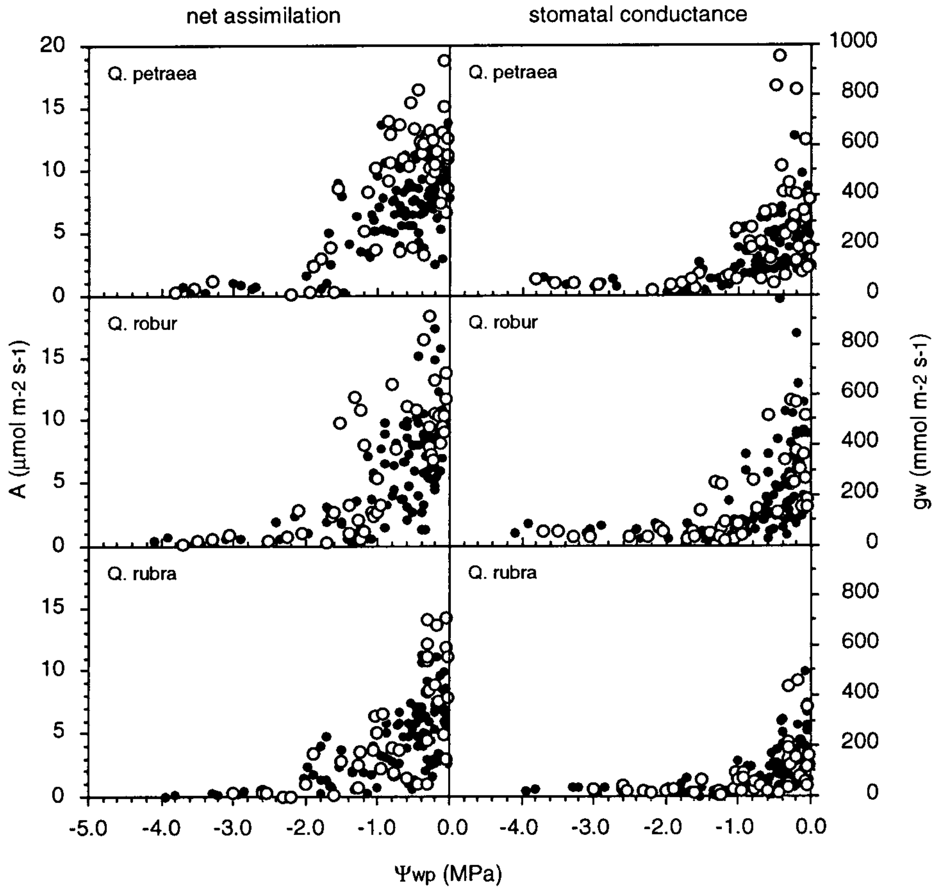

Fig 2. Evolution of net assimilation rate per unit leaf area (*A*, μmol m^{-2} s^{-1}) and leaf stomatal conductance to water vapor (g_w, mmol m^{-2} s^{-1}) in relation to predawn leaf water potential (ψ_{wp}, MPa) for the 3 oaks. Full and open symbols represented unfertilized (u) and fertilized (f) treatments respectively.

plant, of leaf, genetic factors) and also by different daily microclimate conditions.

As ψ_{wp} decreased, so did A and g_w. Nearly complete stomatal closure was reached at ≈ −1.8 MPa for both indigenous oak species and at −1.6 MPa for *Q rubra*. During the drought period, A fell to nearly zero for ψ_{wp} values < −2.8 MPa for the 3 oak species.

Because of the wide variation in gas exchange of plants in response to ψ_{wp}, selected analyses were performed on plants grouped according to predawn water potential classes: 1) well watered (0 to −0.75 MPa); 2) moderately stressed (−0.75 MPa to −1.25 MPa); 3) stressed (−1.25 MPa to −1.75 MPa); 4) severely stressed (−1.75 MPa to −2.50 MPa); and 5) very severely stressed (< −2.50 MPa). Selection of these classes was based on an assessment of scattered plots of gas exchange *versus* predawn water potentials. Analysis of variance (with Fisher PLSD) was used to determine the significance of relationships between gas exchange values and water status.

As shown in figure 3, the 2 indigenous oaks displayed a similar mean net assimilation rate (respectively 8.09 ± 0.29 µmol m^{-2} s^{-1} for *Q petraea* and 7.68 ± 0.41 µmol m^{-2} s^{-1} for *Q robur*) in well watered conditions (class 1). In contrast, *Q rubra* presented a significant lower value (5.73 ± 0.30 µmol m^{-2} s^{-1}). Analog findings were

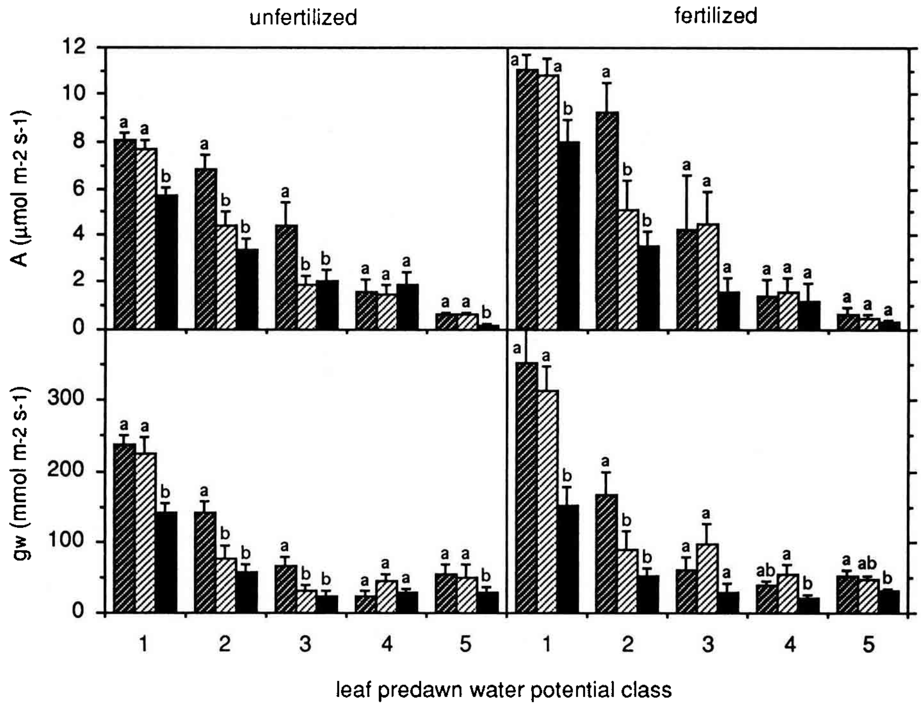

Fig 3. Effect of species on mean net assimilation rate per unit leaf area (± SE) (A, µmol m^{-2} s^{-1}) and leaf stomatal conductance to water vapor (± SE) (g_w, mmol m^{-2} s^{-1}) in relation to predawn leaf water potential class for the 2 nutrition levels (see *Materials and methods* for water potential classes). Two bars with different letters indicate a statistical variation. Species: ▨*Q petraea*; ▨*Q robur*; ■ *Q rubra*.

obtained with the mean value of g_w (237 ± 14 mmol m^{-2} s^{-1} for *Q petraea*, 226 ± 22 mol m^{-2} s^{-1} for *Q robur*, and 142 ± 11 mmol m^{-2} s^{-1} for *Q rubra*). It must be emphasized that *Q petraea* again showed significantly higher values of A and g_w in classes 2 and 3.

The effects of fertilization on gas exchange are summarized in table II. When ψ_{wp} was > –0.75 MPa (class 1), nutrition supply increased mean values of A in the 3 oak species. However, *Q rubra* still displayed a significantly lower value than the 2 indigenous oak species. As ψ_{wp} decreased < –0.75 MPa (other classes), fertilization apparently had no more effect on A/ψ_{wp} relationship. It did not affect mean values of g_w in any species except in *Q petraea* at high leaf water potential.

Shoot elongation

Relative daily elongation (RDE) rate was calculated by first dividing weekly elongation rates of each plant by days separating 2 measurements. This absolute daily shoot increment was then divided by the maximum value for each plant, in order to yield a relative daily elongation rate expressed as a percentage of the maximum value.

Predawn leaf water potential was measured as median value between 2 weekly measurements of shoot elongation. When it was not available, ψ_{wp} was estimated by linear interpolation.

RDE rate/ψ_{wp} relationships are plotted in figure 4. Zero RDE values were not reported in the figure. For each ψ_{wp} hand-drawn contour curves indicated maximum

Table II. Effect of nutrition on mean net assimilation rate per unit leaf area (A, µmol m^{-2} s^{-1}) and leaf stomatal conductance to water vapor (g_w, µmol m^{-2} s^{-1}) in relation to predawn leaf water potential class for the 3 species (see *Materials and methods* for more details). Bold letters indicated statistical variation of Fisher PLSD at 95%.

		Class 1	*Class 2*	*Class 3*	*Class 4*	*Class 5*
Q petraea	Unfertilized	**8.09 a**	6.80	4.43	1.55	0.61
	Fertilized	**11.08 b**	9.27	4.24	1.44	0.66
Q robur	Unfertilized	**7.68 a**	4.41	1.89	1.47	0.60
	Fertilized	**10.82 b**	5.12	4.46	1.54	0.51
Q rubra	Unfertilized	**5.73 a**	3.35	2.04	1.91	0.19
	Fertilized	**7.97 b**	3.49	1.56	1.14	0.33
Stomatal conductance						
Q petraea	Unfertilized	**0.237 a**	0.140	0.065	0.024	0.054
	Fertilized	**0.354 b**	0.168	0.060	0.039	0.053
Q robur	Unfertilized	0.226	0.077	0.032	0.044	0.049
	Fertilized	0.314	0.089	0.098	0.056	0.046
Q rubra	Unfertilized	0.142	0.057	0.023	0.029	0.028
	Fertilized	0.151	0.053	0.029	0.022	0.032

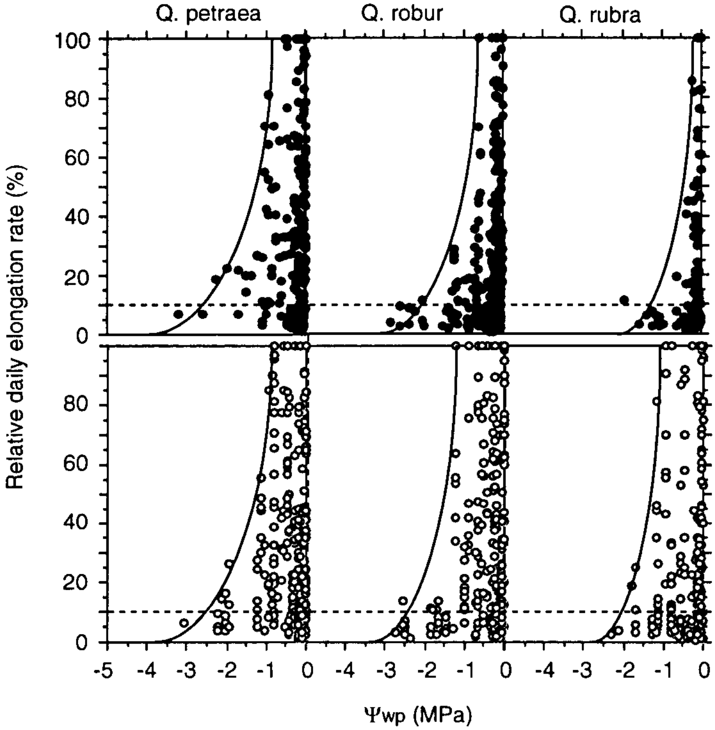

Fig 4. Relative shoot elongation (RDE, percentage of the maximum) in relation to predawn leaf water potential (ψ_{wp}, MPa) for the 3 species. Full and open symbols represented unfertilized (u) and fertilized (f) treatments respectively. Points corresponding to no relative elongation were not shown.

values of RDE rate. Below plotted points were readily explained by unfavorable growth conditions. For simplicity, this graphic representation (*ie* contour curve) provided a possible guide for understanding drought effects on growth while avoiding, at least in part, phenological effects.

For unfertilized plants, maximum RDE rate decreased rapidly from –0.3 MPa for *Q rubra*, –0.6 MPa for *Q robur* and –0.9 MPa for *Q petraea*. Growth became non significant (< 10% of maximum) beyond –1.4 MPa for *Q rubra* –2.0 MPa for *Q robur* and –2.5 MPa for *Q petraea*.

As illustrated in figure 4, fertilization had a positive effect on growth of *Q rubra* and *Q robur* whatever the water treatment, but had no significant effect on *Q petraea*. Growth decreased only beyond –1.0 MPa for the 3 species, and became very low (< 10%) when ψ_{wp} exceeded –2.0 MPa for *Q rubra*, and –2.5 MPa for both indigenous oak species.

These findings suggested that nutrition supply had little influence on growth of *Q petraea* in water deficit conditions; this was to be expected, because *Q petraea* was already resistant enough to water deficit. Conversely, fertilization improved growth of both other oak species. Hence, *Q robur* displayed growth similar to that of *Q petraea*.

Death rate

From August 30 (jd 242), none of the trees were watered. As soon as ψ_{wp} exceeded the minimum value measurable with the pressure chamber (–5.0 MPa), plants were irrigated to field capacity with the aim of observing their survival rates the following year. In Spring 1991, an inventory was made to calculate death rate linked to the 1990 imposed drought. Hence, figure 5 shows that there was no mortality in control treatments, which were only submitted to a late short water stress ($\psi_{wp} > -3.6$ MPa) after jd 242. In contrast, in other unfertilized treatments, *Q robur* showed the highest death rate (18.0%); *Q petraea* (5.6%) and above all *Q rubra* (0.8%) had a lower death rate.

Fertilization had an unexpected negative effect on survival of the 3 species (see fig 5). Death rates were increased while keeping initial ranking. This effect might be due at least in part to difference in biomass productivity.

DISCUSSION

This study, carried out under semi-natural conditions on *Q petraea*, *Q robur* and *Q rubra* saplings grown in boxes and submitted to soil drought cycles, had 2 aims: i) to analyse differences in drought responses of both pedunculate and sessile oaks, so as to understand differences observed in the forest; and ii) to compare northern red oak with the 2 indigenous oaks.

Generally, most oaks have deep-penetrating root systems, enabling them to maintain relatively high predawn potentials during drought (Abrams, 1990). Thus, a deep root system may be considered as a primary adaptation which allows oaks to

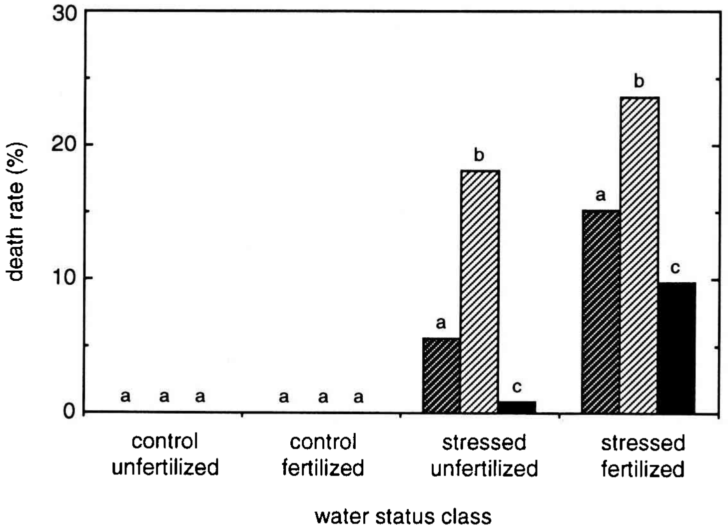

Fig 5. Mean death rate in relation to the different treatments for the 3 species. For each treatment, 2 different letters indicate a statistical variation. Species: ▨ *Q petraea*; ▧ *Q robur*; ■ *Q rubra*.

avoid dessication during drought. In the present study, trees had an available soil depth of 1 metre, so the root system of our 5-yr-old plants was less confined than if they had been in small-sized pots. Consequently, it was possible to extrapolate from these results to natural conditions.

The experimental design allowed new information to be obtained, especially since species were studied in pairs. In each box, ψ_{wp} temporal evolution was the same for the 2 species, thus allowing interspecific comparison of avoidance and resistance.

Drought effects

Leaf gas exchange in *Quercus* was sensitive to water stress, as drought clearly induced a decrease in net CO_2 assimilation rate and stomatal conductance. Net photosynthesis became non significant as ψ_{wp} reached –2.8 MPa for any oak species. Very similar results have been reported with *Q petraea* seedlings, showing an identical decrease of gas exchange during drought, with a total inhibition of photosynthesis at –3.0 MPa (Colleu, 1983; Epron and Dreyer, 1990).

Nearly complete midday stomatal closure was attained when ψ_{wp} reached –1.8 MPa. However, *Q rubra* stomata closed earlier (–1.6 MPa); and these species seemed more sensitive to water deficit than both indigenous oak species. Yet such claims could be dubious. The differentiation between species *via* gas exchange responses to drought was rather difficult.

Concerning the mechanisms involved the stomatal effect was critical to initial reduction of *A* through decreasing intercellular concentrations of CO_2 as ψ_{wp} fell. Moreover, according to a number of scientists, it was likely that simultaneous mesophyll effects took place, causing an alteration in photosynthetic capacity. However, Epron and Dreyer (1990) revealed that the photosynthetic system strongly resisted leaf water deficits, and considered that photoinhibition could be an important factor in explaining photosynthetic system sensitivity to drought. But according to the results of Weber and Gates (1990) on *Q rubra* and those of Epron *et al* (1992) on *Q petraea*, it seemed that no photoinhibitory damage could be detected in water-stressed oak before total reduction of *A*. So in the present study it appeared that early drought effects were mainly mediated by stomatal closure.

As ψ_{wp} decreased, so did growth in all oak species as noted above. In the case of the unfertilized plants, the RDE fell quickly, usually from –0.3 MPa for *Q rubra*, –0.6 MPa for *Q robur* and –0.9 MPa for *Q petraea* and became non significant (< 10%) below –1.4 MPa for *Q rubra*, –2.0 MPa for *Q robur* and –2.5 MPa for *Q petraea*. In previous experiments on *Q robur*, Aussenac and Levy (1983) found a total growth inhibition when ψ_{wp} reached –1.1 MPa. Could this difference be meaningful? In fact in the present study, by taking a contour curve, the RDE rate of *Q robur* reached 20% when ψ_{wp} dropped to –1.2 MPa. Furthermore, in a tree with short shoot elongation, each error in its measurement (± 1 mm) resulted in high variation of RDE rate. In other words, points should be regarded cautiously due to possible variations on the *X* and *Y* axes. Nevertheless, this representation seemed suitable for characterization of growth response to drought.

Concerning resistance to very high water deficit (many drought cycles), large differences occurred between species. Death rate was higher in *Q robur* than in *Q petraea*; *Q rubra* remained unaffected. However, for all species, no mortality was observed as control treatments were submitted to a short drought period at the end of summer. Thus for the first time in such experiments, results closely resembled forest observations. In fact, data not quoted above revealed that at identical ψ_{wp}, yellowing and withering status occurred earlier in *Q robur* than in *Q petraea*, suggesting that *Q robur* avoided drought. But given the mortality rate, the higher sensitivity of *Q robur* seems mainly due to lower tolerance to water stress.

In connection with the tolerance hypothesis and survival rate for drought, it must be emphasized that Cochard *et al* (1992) showed a difference in the sensitivity of vessels to embolism, providing a possible explanation of forest observations.

Nutrition supply effects

Fertilization only increased *A* in all oak species when plants were well watered. It did not affect *A* or g_w in any species when ψ_{wp} was < -0.75 MPa, except for *Q petraea* (see *Results*). Some researchers reported similar results on different plant species grown with high or low nitrogen supply: a large difference in *A* at high leaf water potential and practically no difference at low ψ_{wp}.

By taking the contour curve, RDE rate was still 100% when ψ_{wp} reached -1.0 MPa in any species. Under well watered conditions, fertilization had only a positive effect on RDE rate for *Q robur* and *Q rubra*. This result could be due to the fact that, as shown in the forest, growth of *Q petraea* is less affected by mineral deficit than that of *Q robur*.

As drought increased, RDE rate decreased less rapidly than in the case of unfertilized plants, except in *Q petraea*. Hence, under water stress conditions, fertilization had an essentially positive effect on both northern red and pedunculate oak species. Thus, nutrition supply seem to favour growth at lower water potential, indicating possible influence of osmoregulation phenomena, in particular for *Q robur* and *Q rubra*. With reference to the abovementioned results observed by Aussenac and Levy (1983), mineral nutrition level was presumably higher in the present study even in the unfertilized treatments.

In conclusion, it was now possible, at least for young plants, to put forward a hypothesis about the differential behaviour of indigenous oak species with respect to water stress. In particular, there was no difference in gas exchange regulation between *Q robur* and *Q petraea*. The 2 species differed in their survival rate to very severe water stress, and this agreed with observed differences by Cochard *et al* (1992) on the sensitivity of their vessels to embolism.

Finally, results of this study confirmed the commonly held opinion that *Q rubra* is a drought-resistant species. Nevertheless, its growth could be strongly affected by a water deficit. In addition, contrary to earlier claims (Kolb *et al,* 1990), *Q rubra* had a good response to nutrients: fertilization had very positive effect on its growth, especially when this species is confronted with soil drought.

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