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Original article

A comparison of photosynthetic responses to water stress in seedlings from 3 oak species: *Quercus petraea* (Matt) Liebl, *Q rubra* L and *Q cerris* L

D Epron, E Dreyer *, G Aussenac

Laboratoire de bioclimatologie et d'écophysiologie forestières, INRA Nancy,
Champenoux, 54280 Seichamps, France

Summary — Photosynthetic responses of oak seedlings (*Quercus petraea, Q rubra* and *Q cerris*) to drought were investigated using gas-exchange and chlorophyll fluorescence. Decreases in predawn leaf water potential (ψ_{wp}) led to pronounced reductions in both stomatal conductance (g_w) and net CO_2 assimilation rate *(A)*. In contrast, the maximal photochemical efficiency of photosystem II (PS II) measured predawn (F_v/F_m) remained unaffected until complete cessation of CO_2 assimilation. Responses of PS II photochemical efficiency ($\Delta F/F_{m'}$) to increasing photon flux density *(PFD)* were determined for leaves of both control and water-stressed seedlings. Drought resulted in a stronger reduction of $\Delta F/F_{m'}$ at a given *PFD* in *Q rubra* and *Q petraea*, but not in *Q cerris*, and led to an overreduction of the primary electron acceptor pool (decrease in photochemical quenching, q_p). Such behavior could explain the observed increase in sensitivity to photoinhibition when these 2 species were water-stressed. In contrast, drought did not promote such an increase in the susceptibility of *Q cerris* leaves to photoinhibition.

chlorophyll fluorescence / oak / photosynthesis / drought / photoinhibition

Résumé — Comparaison de la réponse au déficit hydrique de la photosynthèse de semis de 3 espèces de chêne : *Quercus petraea* (Matt) Liebl, *Q rubra* L et *Q cerris* L. *La réponse de la photosynthèse à la sécheresse a été étudiée sur des semis de chêne (*Quercus petraea, Q rubra *et* Q cerris*) par des mesures d'échange gazeux et de fluorescence de la chlorophylle. La diminution du potentiel hydrique de base (ψ_{wp}) a entraîné une réduction importante de la conductance stomatique (g_w) et de l'assimilation nette de CO_2* (A). *Par contre, l'efficience photochimique maximale du PS II mesurée en fin de nuit (F_v/F_m) n'a pas été affectée tant qu'un arrêt complet de l'assimilation de CO_2*

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* Correspondence.

Abbreviations: **A**: net CO_2 assimilation rate; g_w: stomatal conductance to water vapour; ψ_{wp}: predawn leaf water potential; π_0: osmotic potential at full turgor; ψ_{wtl}: water potential at turgor loss; **D**: leaf water deficit; **PS II**: photosystem II; **QA**: primary electron acceptor; F_0 and F_m: initial and maximal fluorescence; F_v/F_m: maximal photochemical efficiency of PS II in the dark-adapted state; $\Delta F/F_{m'}$: photochemical efficiency of PS II in a light-adapted state; $F_{v'}/F_{m'}$: photochemical efficiency of open PS II reaction centers in a light-adapted state; q_P: photochemical fluorescence quenching; ***PFD***: photon flux density.

n'était pas intervenu. Des réponses de l'efficience photochimique du PS II ($\Delta F/F_{m'}$) *à une augmentation de la densité de flux quantique* (PFD) *ont été établies pour des feuilles de semis irrigués et soumis à sécheresse. Le déficit hydrique a entraîné une plus forte réduction de* $\Delta F/F_{m'}$ *à un* PFD *donné pour* Q rubra *et* Q petraea, *s'accompagnant d'une plus forte réduction du pool d'accepteurs primaires d'électrons (diminution du quenching photochimique,* q_p*). Ce comportement pourrait expliquer l'augmentation de la sensibilité à la photo-inhibition des feuilles des plants soumis à sécheresse de ces 2 espèces. Au contraire, la sécheresse n'a pas entraîné de différence de réduction du pool d'accepteurs primaires d'électrons, ni de la sensibilité à la photo-inhibition des feuilles de* Q cerris.

fluorescence de la chlorophylle / chêne / photosynthèse / sécheresse / photo-inhibition

INTRODUCTION

Oak species are distributed over a large geographic range and display great variations in their abilities to tolerate periods of restricted water supply. This latter factor probably plays a major role in the control of the distribution of the various oak species. Some species have evolved very specialized adaptive features which are thought to enable better survival under drought, such as sclerophylly, restricted area of individual leaves and thick cuticles. However, even among the more mesophytic and deciduous species, some important differences in tolerance to drought appear. For instance, thorough ecological studies showed that *Q robur* and *Q petraea* had different water supply requirements, the former being more sensitive to drought and, as a consequence, more prone to drought-induced decline (Becker and Lévy, 1982). Nevertheless, the physiological mechanisms involved in this differentiated water stress tolerance are still poorly understood. Efficiencies of soil water extraction and of water transport pathways in the trees probably play a major role and differ significantly among species (Abrams, 1990; Cochard *et al*, 1992; Bréda *et al*, 1993). In addition, the ability to maintain significant rates of CO_2 assimilation and to keep a functional photo-synthetic apparatus during drought may have an important role in this respect.

Drought-induced stomatal closure is now well documented. In many recent studies it has been reported to be the primary factor promoting the decrease in net assimilation rates during drought (kaiser, 1987; Cornic *et al*, 1989). Moreover, the photosynthetic apparatus and in particular, the potential photochemical activity of PS II, has been shown to be highly insensitive to rapid leaf dehydration in the dark for *Q petraea* (Epron and Dreyer, 1992) and for a large spectrum of species (Dreyer *et al*, 1992). Rapid leaf dehydration does not affect photochemistry above degrees of dehydration only rarely attained under natural conditions.

Still, the question remains as to whether gradually increasing drought can affect the photosynthetic processes when it is imposed under medium or high irradiance. In particular, the relationship between water-stress intensity and light-induced disorders in PS II activity still has to be clearly assessed. Chlorophyll *a* fluorescence may be used to estimate quantum efficiencies of PS II under diverse environmental constraints (Baker, 1991) and is therefore a useful tool to study physiological consequences of drought on photosynthetic electron transport.

To test responses of different oak species to a combination of water stress and high irradiance, we subjected potted seedlings to a gradually increasing drought and monitored predawn leaf water potential, gas exchange and photochemical efficiency of PS II. Selected species were *Q cer-*

ris, a SE European species known to be relatively drought tolerant, *Q petraea*, an important mesophytic timber species of W Europe and *Q rubra*, a NE American species probably slightly more sensitive to drought. *Q cerris* has the thickest leaves and bears a high amount of trichomes; *Q petraea* has been shown to be less prone to drought-induced embolism than *Q rubra* (Cochard *et al*, 1992).

MATERIAL AND METHODS

Seedlings of *Quercus petraea* (Matt) Liebl (Forêt de la Reine, Toul, NE France), *Q cerris* L (commercial seedlots) and *Q rubra* L (Fénétrange, NE France) were grown in a naturally illuminated greenhouse from March to September 1990, in 5-l pots filled with a 1:1 (v/v) mixture of sand and blond peat, fertilized with 2.0 g of Nutricote 100 (N/P/K: 13/13/13) and complemented with a mixture of oligoelements, and 4 g of magnesium chalk. The plants were irrigated daily. One week before the onset of the experiments, the seedlings were transported into a growth cabinet with the following day/night conditions: 16/8 h; relative humidity, 70/95%; air temperature, 22/16 °C. Photosynthetic photon flux density (*PFD*) provided by neon lamps was around 200 μmol m^{-2} s^{-1} at the top of the plants.

Stress application and experimental design

Drought was imposed on 6 seedlings from each species by withholding irrigation for 9 days. Predawn leaf water potential (ψ_{wp}), relative water content, gas exchange and chlorophyll *a* fluorescence characteristics were monitored every day on half of the plants on the last fully developed growth flush. Three plants were kept as controls.

Responses of photochemical efficiency to increasing *PFD* and susceptibility to high light stress were studied on 3–4 leaf disks (10 cm^2) punched from either well-watered or water-stressed plants (predawn leaf water potential $\psi_{wp} \approx -3.0$ MPa in the latter case). Each leaf disk was inserted into the compartment of a leaf-disk O_2 electrode (Hansatech, UK). A stream of water-vapor saturated air, maintained at 23°C, and with ambient CO_2, was sufficient to prevent dehydration or heating of leaf tissues. *PFD* was changed every 10 min from 135 to 230, 460, 890, 1300 and 1750 μmol m^{-2} s^{-1}. Then, the leaf disk was exposed to a *PFD* of 1750 μmol m^{-2} s^{-1} for 135 min and finally put in the dark for 45 min to determine long-term changes in maximal photochemical efficiency.

Leaf water status

Predawn leaf water potential (ψ_{wp}) was measured with a pressure chamber on a single leaf of each seedling, while relative water content was estimated from 2 disks punched through this leaf prior to introduction into the pressure chamber.

The 2 leaf disks (2 cm^2) were immediately weighed (W_f), used for fluorescence measurements, rehydrated by floating on distilled water for 4 h at 4 °C in the dark to determine saturated weight (W_s) and oven-dried for 24 h at 80 °C to determine dry weight (W_d). Relative water content was calculated as $RWC = (W_f - W_d)/(W_s - W_d)$; and leaf water deficit expressed as $D = 1 - RWC$.

Osmotic potential at full turgor (π_o) and water potential at turgor loss (ψ_{wtl}) were assessed on well-watered controls by means of a pressure–volume analysis using the transpiration method described by Hinckley *et al* (1980) and Dreyer *et al* (1990). Three shoots were severed from 3 well-watered seedlings of each species and rehydrated overnight through the cut end. Water potentials of freely transpiring shoots (ψ_w) were measured at regular time intervals from 0 to –6.0 MPa in a pressure chamber. Shoot weight was recorded to calculate shoot water deficit as: $D = 1-[(W_f - W_d)/(W_i - W_d)]$, where W_f, W_i and W_d represent respectively, shoot weight measured immediately after ψ_w determination, initial weight of the rehydrated shoot and dry weight of the shoot.

Gas-exchange measurements

Stomatal conductance for water vapour (g_w) and net CO_2 assimilation rate *(A)* were recorded using a portable gas-exchange measurement system (LiCor 6200, Lincoln, NE, USA). Average (± standard deviation) leaf temperature (t_a), leaf-to-air difference in vapor mol fraction, CO_2 mole fraction in the air (c_a), and *PFD* at the leaf surface were, respectively, 23.9 (± 0.9)°C, 11.6 (± 3.3) mmol mol^{-1}, 440 (± 24) µmol mol^{-1} and 194 (± 22) µmol m^{-2} s^{-1}. Both *A* and g_w were computed according to von Caemmerer and Farquhar (1981) and expressed on a projected leaf-area basis (ΔT area meter, ΔT Devices, UK). Measurements were made 3–4 h after the onset of the light period.

Chlorophyll a fluorescence measurement

Chlorophyll *a* fluorescence of PS II was measured using a pulse amplitude modulated fluorometer (PAM 101, Walz, Germany) as previously described (Epron and Dreyer, 1992). Leaf disks (2 cm^2) were punched from overnight dark-adapted seedlings. Initial fluorescence (F_o), when all PS II reaction centers were open, was obtained using a weak light (less than 1 µmol m^{-2} s^{-1}) from a light-emitting diode (λ_{max}, 650 nm; pulse duration, 1 µsec; frequency, 1.6 kHz). Maximum fluorescence (F_m) when all PS II reaction centers were closed, was recorded during a flash of saturating white light (4000 µmol m^{-2} s^{-1}). Maximal photochemical efficiency of PS II, *ie*, in the dark-adapted state, was calculated according to Genty *et al* (1987) as: $F_v/F_m = (F_m - F_o)/F_m$.

Photochemical efficiency of PS II was determined during the establishment of light response curves, after 10 min at each successive *PFD* (135, 230, 460, 590, 1300 and 1750 µmol m^{-2} s^{-1}). Steady-state fluorescence (*F*) and maximal fluorescence following a saturating flash ($F_{m'}$) were recorded and used to compute the photochemical efficiency of PS II as: $\Delta F/F_{m'} = (F_{m'} - F)/F_{m'}$ (Genty *et al*, 1989). After each 10-min period, the actinic light was switched off for 1 min to allow recording of basic fluorescence $F_{0'}$ and to compute photochemical efficiency of open PS II reaction centers as: $F_{v'}/F_{m'} = (F_{m'} - F_{0'})/F_{m'}$ (Genty *et al*, 1989). The two parameters are related by the equation: $\Delta F/F_{m'} = q_p \bullet F_{v'}/F_{m'}$; where q_p is the photochemical quenching, *ie* the fraction of open PS II reaction centers. Decreases in q_p are generally ascribed to increased reduction of the primary acceptor Q_A, while decrease of $F_{v'}/F_{m'}$ are thought to reveal enhanced thermal deexcitation of PS II (Baker, 1991).

To test the effects of high light stress we compared F_v/F_m before exposure to light and after a complete *PFD* response curve followed by an additional 135 min at 1750 µmol m^{-2} s^{-1} and 45 min darkness.

RESULTS

Drought progression and plant water status

During the first 4 days, soil water content decreased from 0.5 to 0.2 g^{-1} of dry weight without any significant decrease in predawn leaf water potential ψ_{wp}. Thereafter, ψ_{wp} declined steadily and reached values below –6.0 MPa 5 days later.

Table I. Water relations of leafy shoots of seedlings from the 3 species as measured using pressure volume relations.

Species	π_0 *(MPa)*	D*tl*	ψ_{wtl} *(MPa)*
Q cerris	–2.14 (0.15) [a]	0.133 (0.036)	–2.51 (0.24)
Q petraea	–1.61 (0.10)	0.141 (0.014°	–1.85 (0.06)
Q rubra	–1.71 (0.04)	0.123 (0.013)	–2.07 (0.07)

[a] Standard deviation. π_0: osmotic potential at full turgor; *Dtl*: leaf water deficit at turgor loss; ψ_{wtl}: leaf water potential at turgor loss.

Decreases in ψ_{wp} led to increases in leaf water deficit, *D* after an initial period of marked variability. But the relationship between *D* and ψ_{wp} displayed some interspecific differences: for a given value of ψ_w, *Q rubra* displayed higher deficits than the other 2 species (fig 1). For example, a ψ_{wp} of about –3 MPa was accompanied by a *D* for ≈ 0.26 in *Q cerris* and *Q petraea*, but of ≈ 0.30 in *Q rubra*.

Osmotic potential at full turgor (π_0) and leaf water potential at turgor loss (ψ_{wtl}) measured on well-watered seedlings are presented in table I. *Q cerris* displayed significantly lower π_0 and ψ_{wtl}, while the other 2 species behaved similarly. A discrepancy between these data and the *D* – ψ_{wp} relationship, as presented in figure 1, appeared for all species: *D* for a given value of ψ_w was always higher (lower water content) during the progression of dehydration than during the establishment of pressure–volume relationships with well-watered seedlings. This may be due either to shifts

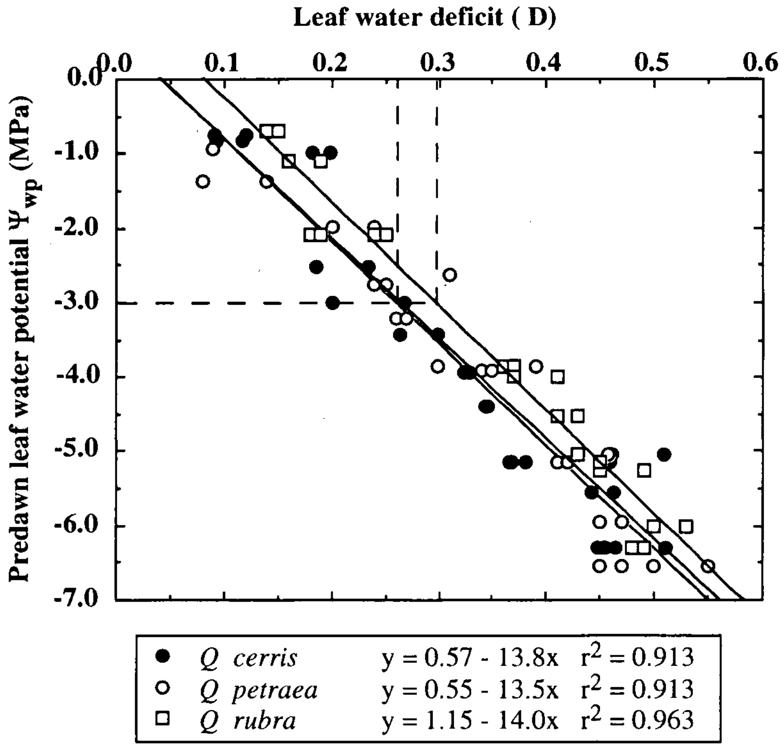

Fig 1. Relationship between predawn leaf water potential (ψ_{wp}) and leaf water deficit *(D)* during drought progression on young potted seedlings from 3 oak species. Linear regression analysis of each data set yielded the equations given.

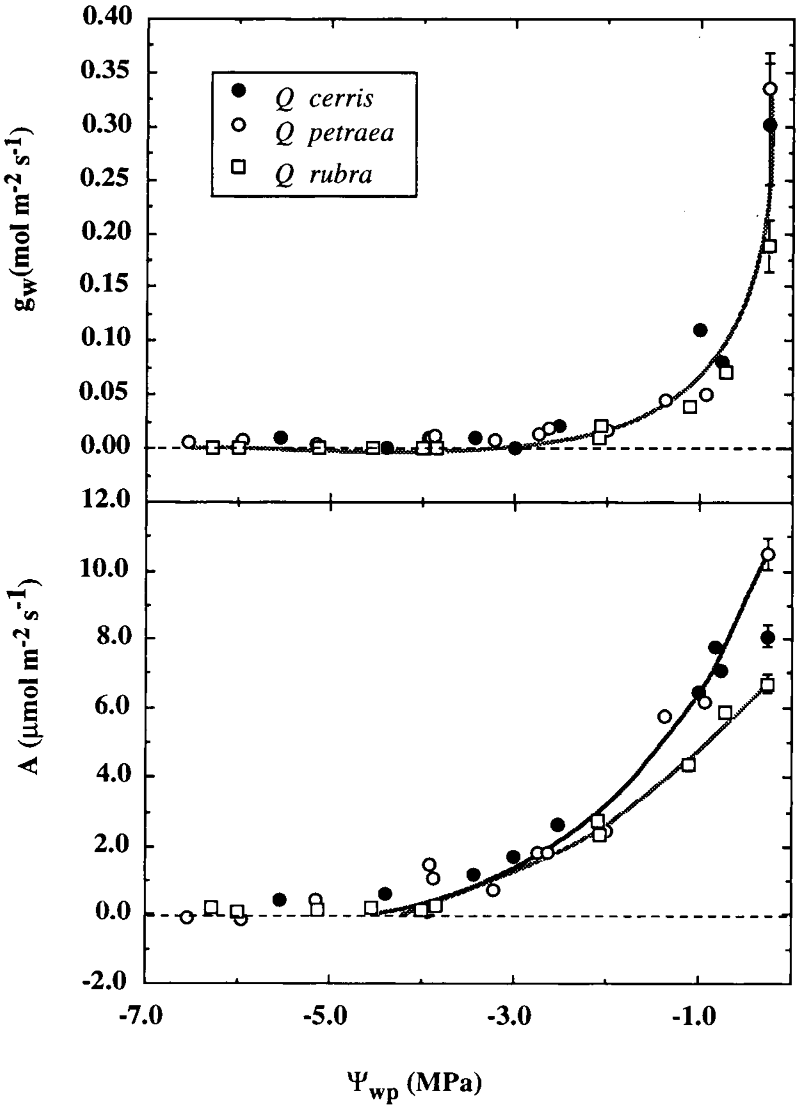

Fig 2. Evolution of stomatal conductance to water vapor (g_w) and net CO_2 assimilation rate *(A)* as a function of predawn leaf water potential (ψ_{wp}) on seedlings from 3 oak species. Each point represents an individual measurement for drought-exposed plants; controls ($\psi_{wp} > -0.5$ MPa) are presented as mean values with confidence intervals. (Conditions: ta: 23.9 °C, PFD: 194 μmol m^{-2}.s^{-1}, ca: 440 μmol mol^{-1}). Lines were fitted by hand to illustrate tendencies.

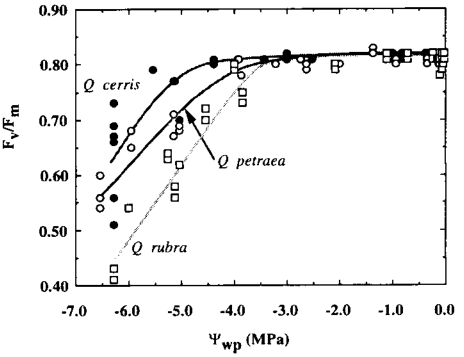

Fig 3. Evolution of maximal photochemical efficiency *(F_v/F_m)* as a function of predawn leaf water potential (ψ_{wp}) on seedlings from 3 oak species. Each point represents an individual measurement. Lines were fitted by hand to illustrate tendencies.

in osmotic potential induced by the drought treatment or to oversaturation of the leaf disks.

Drought effects on stomatal conductance and net CO_2 assimilation rate

Stomatal conductance to water vapor (ψ_w) and net CO_2 assimilation rates *(A)* displayed large species-related differences on well-watered seedlings (fig 2): *Q petraea* reached the highest rates of *A* and g_w, followed by *Q cerris* and *Q rubra*. All 3 species exhibited similar rates of change in *A* and g_w as ψ_{wp} decreased. Decreases in *A* began above −1.0 MPa but were gradual. Values close to zero were obtained in all cases when ψ_{wp} reached −3.5 MPa. The decline of g_w was much steeper, reaching values below 0.025 mol m^{-1} s^{-2} at −1.5 MPa in all species. Differences in the decline rates of g_w and *A* may be due to CO_2 limitation of *A* and supra-optimal stomatal conductance on well-watered seedlings.

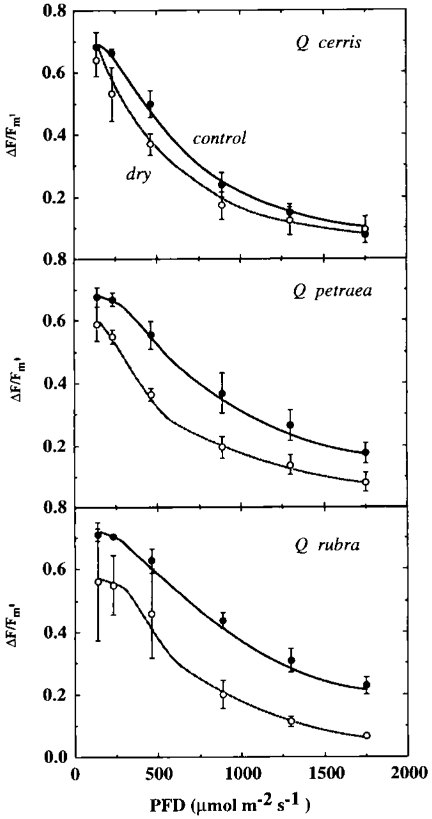

Fig 4. Relationship between incident photon flux density *(PFD)* and PS II photochemical efficiency *($\Delta F/F_m'$)* on control (●) and stressed (○) leaves of seedlings from 3 oak species. Predawn leaf water potential of stressed seedlings was −3.0 ± 0.2 MPa in all cases. Means of 4 measurements ± standard deviation. Lines were fitted by hand to illustrate tendencies.

Drought effects on photochemical efficiency of PS II

Responses of maximal photochemical efficiency of PS II (F_v/F_m) to declining ψ_{wp} are shown in figure 3. F_v/F_m remained high and constant (≈ 0.81) in all species until ψ_{wp} dropped below −4.0 MPa. Such low potentials correspond to values of *D* >

0.35. The observed decreases resulted from both a decrease in F_m and an increase in F_0 (data not shown). Low F_v/F_m values of ≈ 0.5 were reached at the lowest water potentials. It is worth noting that these decreases began at stress intensities for which net assimilation rates were almost nil. Some marked species-related differences were clear: the drought-induced decline appeared at lower water potentials in *Q cerris* than in the other 2 species.

Drought effects on light-response curves of PS II photochemical efficiency

Responses of PS II photochemical efficiency ($\Delta F/F_{m'}$) to increasing *PFD* are shown in figure 4. As expected, $\Delta F/F_{m'}$ was high at low irradiance, and decreased steadily with increasing *PFD* in both controls and water-stressed seedlings. Final values of controls (at 1750 µmol m^{-2} s^{-1}) were ≈ 0.20 for *Q petraea* and *Q rubra*, but < 0.10 for *Q cerris*. Water stress had strong consequences in the 2 former species, inducing much lower $\Delta F/F_{m'}$ at a given irradiance as compared to controls. In *Q cerris* no significant difference was observed between both situations. The same relationship between $\Delta F/F_{m'}$ and $F_{v'}/F_{m'}$ or q_p was observed in all species independently of the drought treatment (fig 5), which may be interpreted as the maintenance of the same equilibrium, at a given efficiency, between thermal deexcitation of PS II and the reduction status of the primary acceptor pool.

Drought effects on response to high irradiance

Table II shows the effects of 135 min of exposure to high light on F_v/F_m for both the control and the water-stressed (–3.0 MPa) seedlings already tested for *PFD* responses (see above). Large decreases of F_v/F_m as measured after 45 min of darkness were detected in all cases. But these decreases were more pronounced on stressed seedlings than on well-watered ones for both *Q petraea* and *Q robur*, but not for *Q cerris*, for which the decreases reached the same extent in both cases. Decreases in F_v/F_m were always the consequence of both a slight increase in F_0 (about 10%) and a strong decrease in F_m (30% minimum).

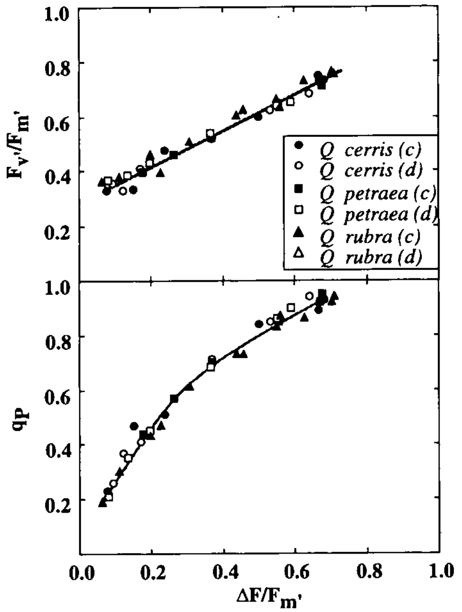

Fig 5. Relationship between PSII photochemical efficiency $(\Delta F/F_{m''})$ and photochemical efficiency of open PSII reaction centers $(F_{v'}/F_{m'})$ or photochemical fluorescence quenching (q_p) as measured on control (c) or dehydrated (d) leaves of seedlings from 3 oak species under increasing incident photon flux density. Lines were fitted by hand to illustrate tendencies.

DISCUSSION

Interspecific variability at optimal water supply

Our species displayed marked differences in behavior at optimal water supply. Net CO_2 assimilation rates per unit leaf area (*A*) were highest on *Q petraea* and *Q cerris*, and lowest on *Q rubra*. Differences in chlorophyll contents, leaf-specific weight and leaf optical properties could partly explain these differences in *A*. Lin and Ehleringer (1982) reported that changes in spectral properties of leaves of papaya associated with differences in chlorophyll contents were strongly correlated to the rate of net CO_2 assimilation. Leaves of *Q rubra* seedlings grown in a glasshouse are known to have lower chlorophyll contents and specific leaf weights than the 2 other species (Dreyer *et al*, 1992). This latter species also exhibited lower stomatal conductance (g_w). Similar differences in *A* and g_w between *Q petraea* and *Q rubra* have already been reported (Vivin *et al*, 1993). It is worth noting that, under such conditions, the intrinsic water-use efficiency ratio (A/g_w) of *Q rubra* was higher than that for *Q petraea* and *Q cerris* (35.6, 31.2 and 26.8 μmol CO_2 mol^{-1} H_2O, respectively). Differences in leaf structure and their consequences on leaf optical properties and on photosynthetic efficiency among oak species clearly need to be better documented; moreover, the impacts of the light regime and microclimate during leaf expansion require further elucidation. The data presented apply to greenhouse-grown seedlings, and a direct extrapolation to natural conditions would be questionable. Nevertheless, despite differences in *A*, maximal photochemical efficiency of PS II was identical in all species.

Water relationships were also very different between the tested species. *Q cerris* had the lowest osmotic potential at full turgor (π_0) and, as a consequence, the lowest water potential at turgor loss. The observed values of π_0 were relatively high when compared to trees grown under natural condi-

Table II. Optimal photochemical efficiency (F_v/F_m) of leaves from well irrigated ($\psi_w > -0.30$ MPa) and droughted ($\psi_{wp} < -2.9$ MPa) seedlings of 3 oak species grown in a glasshouse as measured either on dark-adapted leaves (8 h darkness) or on the same leaves after 135 min of exposure to high irradiance (1750 μmol m^{-2} s^{-1}) followed by 45 min of darkness.

Species	ψ_{wp} *(MPa)*	F_v/F_m		*Decline (%)*
		Before	*After*	
Q cerris	−0.28 (0.03) [a]	0.82 (0.01)	0.73 (0.01)	12
	−3.05 (0.41)	0.80 (0.01)	0.69 (0.02)	14
Q petraea	−0.09 (0.02)	0.81 (0.01)	0.70 (0.03)	14
	−2.91 (0.39)	0.81 (0.01)	0.64 (0.03)	21
Q rubra	−0.05 (0.01)	0.81 (0.01)	0.71 (0.01)	13
	−3.10 (0.19)	0.80 (0.01)	0.60 (0.02)	24

[a] Standard deviation.

tions, but in agreement with already published data for mesophytic oaks grown in the greenhouse (Dreyer *et al*, 1990).

General reactions to drought

All species exhibited an abrupt decline in stomatal conductance as soon as ψ_{wp} decreased from values near 0 to −1.0 MPa. Decreases in *A* were much more gradual. An important consequence was that intrinsic water-use efficiency increased during the initial stages of progressive dehydration, as has been frequently reported (Schulze and Hall, 1982; Epron and Dreyer, 1990, for other oak species). Our results suggest a rather good ability of oak species to maintain significant rates of *A* during drought progression, as already shown by Epron and Dreyer (1990) for potted saplings or under natural conditions by Hinckley *et al* (1978), Bahari *et al* (1985) and Epron *et al* (1992).

Recent results suggest that the photosynthetic apparatus is rather tolerant to dehydration (Kaiser, 1987; Cornic *et al*, 1989; Epron and Dreyer, 1990, 1992), and that drought effects seem to be mainly mediated by stomatal closure, at least at the levels commonly experienced under field conditions. In particular, maximal photochemical efficiency (F_v/F_m), measured on dark-adapted oak leaves during rapid dehydration, remained constant until very high leaf–water deficits ($D \approx 0.75$) (Epron and Dreyer, 1992). In our case, on potted seedlings drying out in a climate chamber, the decline in F_v/F_m appeared at lower deficits ($\psi_{wp} \approx -4$ MPa, that is $D \approx 0.35$). F_v/F_m was measured at predawn, which should have allowed overnight relaxation of daily changes in potential PS II activity. Under field conditions, Epron *et al* (1992) observed on stressed trees that predawn F_v/F_m was always near optimal values, despite dramatic but reversible reductions during periods of highest irradiance. Weber and Gates (1990) showed the lack of permanent photo-inhibitory damage on *Q rubra* subjected to drought, despite the strong reduction in *A*. But, during these field experiments, water stress never induced complete arrest of photosynthetic carbon assimilation. It can be inferred from these observations that marked decreases of potential PS II activity may occur only during periods of complete cessation of assimilation and under intense irradiance. As the observed decreases resulted from both increased F_0 and decreased F_m, it can be concluded that they were the expression of some kind of damage to the PS II (Demmig and Björkman, 1987). However, these injuries were not directly associated with leaf dehydration, but rather with excess light energy reaching PS II reaction centers when CO_2 assimilation was completely inhibited in severely stressed seedlings.

The lack of damage to PS II in moderately stressed leaves (ψ_{wp} from −1.0 to −4.0 MPa), despite a pronounced decrease in *A*, has already been documented in other species (Ben *et al*, 1987; Genty *et al*, 1987; Di Marco *et al*, 1988). Two complementary mechanisms could help protect PS II from injury: 1) the quantum yield of PS II photochemistry may be transiently reduced by increased thermal energy dissipation when the rate of electron transport exceeds the need of reducing power for CO_2 fixation; this was observed at midday under natural conditions on sun-exposed leaves of oak trees (Epron *et al*, 1992); 2) an increasing part of the electron flow originating from PS II may be diverted from carboxylation to photorespiration, as experimentally demonstrated by Cornic and Briantais (1991).

Response to PFD *and photo-inhibition*

Increasing *PFD* clearly reduced the quantum efficiency of PS II ($\Delta F/F_{m'}$) of both control and water-stressed leaves. However, at all *PFD*, water stress resulted in lower values of $\Delta F/F_{m'}$ in *Q petraea* and *Q rubra*. Lower $\Delta F/F_{m'}$ in stressed individuals was probably induced by low CO_2 availability at the chloroplast level resulting from stomatal closure. The decrease reveals that diversion of electron flow to photorespiration may not have been sufficient to maintain similar rates of PS II photochemistry during drought in these species. These *PFD*-related reductions were always accompanied both by increased thermal deexcitation (reduced $F_{v'}/F_{m'}$) and decreases in q_p, *ie* the pool of primary electron acceptors was gradually reduced. It has to be emphasized that, at any given value of PS II photochemical efficiency, the balance between the increase in thermal deexcitation and the reduction status of the pool of primary electron acceptors (Q_A) was similar in the 3 species tested, and on both control and dehydrated leaves.

We demonstrated that drought also induced an enhancement in susceptibility to high-light stresses. Such effects of drought has previously been observed on many species (*Nerium oleander,* Björkman and Powles, 1984; *Q petraea*, *Q pubescens* but not *Q ilex*, Epron and Dreyer, 1990). In our case, high light favored an alteration in PS II reaction centers, as the reduction in F_v/F_m resulted from both a decrease in F_m and an increase in F_0 (Demmig and Björkman, 1987). This finding clearly distinguishes the reactions observed here from the diurnal and reversible decreases in F_0, F_m and F_v/F_m noted under natural conditions (Epron *et al*, 1992). The reasons for this increased sensitivity to high irradiance due to drought are still open to debate. One explanation may be that CO_2 starvation induced by stomatal closure allowed damaging effects of excess excitation delivered to PS II reaction centers (Powles, 1984). Excess excitation energy may generate highly reactive oxygen species that could be responsible for this damage (Kyle, 1987). However, loss of PS II activity should be observed only if the rate of damage exceeded the rate of repair (Baker, 1991).

Q cerris displayed the least drought-induced sensitivity to high-light stress. Differences in absorbance existed between our species (Epron, unpublished data), but their magnitudes were too limited to explain the observed differences. Demmig *et al* (1988) suggested that the resistance of *Nerium oleander* to photodamage when exposed to a combination of high light and water stress was associated with an increasing ability for radiationless energy dissipation. But we did not detect any interspecific difference in the ability to dissipate excess energy when electron transport was reduced. It has frequently been suggested that photodamage should be enhanced when the Q_A pool is highly reduced (Krause and Weis, 1991). Surprisingly, the Q_A pool at a given *PFD* was reduced more in well-watered *Q cerris* than in the other species, despite similar sensitivities to high-light exposure. Some other mechanisms, for instance higher rates of recovery (Greer *et al*, 1986), may limit the extent of damage to PS II photochemical efficiency in this species. In contrast, differences in sensitivity to high-light exposure between control and dehydrated leaves of *Q rubra* and *Q petraea* were well correlated to lower PS II photochemical efficiency at a given *PFD, ie* a higher reduction state of Q_A. In *Q cerris*, the reduction state of Q_A was similar in well-watered and water-stressed leaves, which was in agreement with the observed lack of increase in sensitivity to high light.

CONCLUSION

Early drought effects seem to be mainly induced by stomatal limitation to photosynthesis. Disorders in the photosynthetic apparatus appeared, nevertheless, at higher stress intensities in all 3 species but were not mediated by leaf-tissue dehydration. The relationships between water stress, high light and species responses need further analysis to elucidate such differential responses. It appears that the drought-induced increase in sensitivity to high light in *Q petraea* and *Q rubra* leaves could be the result of an overreduction of the Q_A pool under high irradiance. *Q cerris*, which did not exhibit such an over-reduction, did not suffer from increased sensitivity to high irradiance. Differences in the abilities of photorespiration to compensate reduction in CO_2 assimilation between our species may be able to explain these differences in drought-induced sensitivity to photoinhibition. Still the higher tolerance to photoinhibition in *Q* cerris at a similar level of Q_A reduction has to be clarified. Moreover, these responses to drought and light may differ on seedlings and trees grown outdoors, which are known to present dramatically different leaf-specific weight and pigment compositions. It remains to be elucidated to what extent irradiance intensity during leaf growth may modulate the stress responses revealed in this work.

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