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Responses of photosynthesis to high temperatures in oak saplings assessed by chlorophyll-a fluorescence: inter-specific diversity and temperature-induced plasticity

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Abstract –

- The sensitivity of photosynthesis to high temperature was investigated in greenhouse-grown saplings of three Mediterranean (*Quercus canariensis* Willd., *Q. coccifera* L. and *Q. suber* L.) and two temperate European oak species (*Q. robur* L. and *Q. petraea* Matt. Liebl.). The sensitivity to high temperature was inferred from F_0T curves producing the critical temperature (T_c) at which a rapid rise in ground chlorophyll a fluorescence (F_0) occurs. T_c is known to acclimate to moderately increased ambient temperature by displaying significant increases.
- We first checked whether acclimation of T_c was paralleled by an increase in optimal temperature for light driven electron flux (T_{opt}), recorded by measuring quantum yield of photochemistry under saturating CO_2 and moderate irradiance. Saplings of *Q. suber* and *Q. canariensis* were submitted to four, five days long ambient temperature steps (15, 25, 35 and 15 °C again). T_c was usually largely above 45 °C while T_{opt} was around 30–35 °C. Both increased with ambient temperature in the two species, and decreased again when temperature returned to the initial values. This recovery was nevertheless not complete after a week at 15 °C.
- A second experiment tested whether the plasticity of T_c was of the same extent in the five species. A significant increase of T_c followed by a decrease was detected in all species. Only small inter-specific differences were detected in T_c , and temperature induced plasticity was similar in the different species: T_c increased by about 4–5 °C while ambient temperature was increased from 15 to 35 °C. Mediterranean and European oaks did not differ in this respect.
- This result does not support the hypothesis that oak species from warmer regions would display a larger plasticity of T_c in response to increasing temperatures.

photochemistry / quantum yield / optimal temperature / *Quercus suber* / *Quercus canariensis* / *Quercus coccifera* / *Quercus robur* / *Quercus petraea*

Résumé – Thermotolérance de la photosynthèse de chênes européens mesurée par la fluorescence de la chlorophylle : diversité interspécifique et plasticité induite par l'acclimatation thermique.

- La sensibilité de la photosynthèse à des températures élevées a été étudiée chez cinq espèces de chênes : trois méditerranéennes (*Quercus canariensis* Willd., *Q. coccifera* L. et *Q. suber* L.) et deux tempérées (*Q. robur* L. et *Q. petraea* Matt. Liebl.). La sensibilité aux fortes températures était estimée suivant la procédure des courbes F_0T par la température critique (T_c) au dessus de laquelle la fluorescence de base de la chlorophylle (F_0) augmente rapidement. T_c présente une forte capacité d'acclimatation et augmente sensiblement après une élévation modérée de la température ambiante.
- Dans une première expérimentation nous avons vérifié si une augmentation de T_c s'accompagnait d'une augmentation de la température optimale du transfert d'électrons durant la photochimie (T_{opt}), estimée par mesure du rendement quantique de la photochimie sous CO_2 saturant sous éclairage modéré. Les jeunes plants de *Q. suber* et *Q. canariensis* ont été soumis à quatre températures ambiantes (15 °C, 25 °C, 35 °C et de nouveau 15 °C) pendant cinq jours. T_c atteignait des valeurs supérieures à 45 °C alors que T_{opt} était aux alentours de 30–35 °C. Chez les deux espèces, ces paramètres ont augmenté avec la température ambiante et à nouveau diminué lors du retour à la température initiale. Nous avons conclu que le changement de la thermostabilité de la photochimie du PSII s'est accompagné d'un changement de la température optimale du transfert d'électrons photosynthétiques.
- Dans une deuxième expérimentation nous avons comparé T_c sur cinq espèces de chêne soumises à la même séquence climatique que précédemment. T_c et sa plasticité différaient très peu entre espèces : T_c a augmenté de 4–5 °C alors que la température ambiante passait de 15 à 35 °C. Les cinq espèces de chênes ne présentaient pas de différences marquées ni de valeur absolue de T_c , ni de plasticité de ce paramètre.
- Ces résultats ne confirment pas l'hypothèse que les espèces méditerranéennes de chêne présenteraient des valeurs plus élevées de T_c , ou une plus forte plasticité de ce paramètre que les espèces de régions tempérées.

fluorescence de la chlorophylle / température optimale / photochimie / *Quercus suber* / *Quercus canariensis* / *Quercus robur* / *Quercus petraea* / *Quercus coccifera*

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1. INTRODUCTION

Mediterranean climate is well known for long lasting periods of drought during summer, with large irradiance loads and temperature maxima that may reach 40 to 45 °C. Such conditions impose strong stresses on leaves of tree species like oaks (Rennenberg et al., 2006). High temperatures above 40 °C, may under circumstances induce leaf necroses and yellowing (Schreiber and Berry, 1977). Among cellular functions, photosynthesis is frequently regarded as one of the most sensitive to high temperatures (Berry and Björkman, 1980). The reversible impact of moderately high temperature (i.e., 35–40 °C) on photosynthetic functions includes rubisco deactivation (Salvucci and Crafts-Brandner, 2004), and inhibition of electron transport capacity but no direct damage to photosystem II (PS II) (see Sharkey, 2005, for an overview). Such reversible effects may be quantified by the temperature inducing a 15% reduction of F_v/F_m , the dark-acclimated quantum yield of photochemistry (Epron, 1997b). Higher temperatures (above 40 °C) may involve direct damage to PSII photochemistry: PSII proteins may be denaturated and thylakoid membrane fluidity may increase to very high levels when temperature reaches critical values (Ducruet et al., 2007; Yordanov, 1992). This critical temperature for PSII functions may be assessed using chlorophyll a fluorescence records and by detecting the leaf temperature at the thermal breakpoint of ground level chlorophyll a fluorescence recorded under darkness (F_0), called critical temperature T_c , (Bilger et al., 1984; Ducruet et al., 2007; Terzaghi et al., 1989). Increased F_0 denotes an inactivation of PS II reaction centres due to thylakoid instability and complex changes in PS II (Cajane et al., 1998; Ducruet et al., 2007). This technique has been used to assess the heat sensitivity of photosynthesis in a number of species (Knight and Ackerly, 2002).

T_c recorded on individuals at a common acclimation temperature displayed only little inter-specific variability in a range of species including Mediterranean and mid European tree species (Froux et al., 2004; Ghoul et al., 2003) or coastal vs desert species in California (Knight and Ackerly, 2002). T_c was usually around 45–50 °C for saplings grown under 20 °C ambient temperature.

Direct interspecific comparisons are made difficult by the fact that T_c is a highly plastic trait (see Ducruet et al., 2007, for a synthesis). T_c can be influenced by a series of environmental parameters like ambient temperature (Dreyer et al., 2001; Havaux, 1993; Robakowski et al., 2002), water availability (Epron, 1997a; Havaux, 1992; Ladjal et al., 2000) and plant growth regulators like ABA (Havaux, 1992; Ivanov et al., 1992). T_c varies largely with season, in parallel to ambient temperatures, and increases during summer and decreases during autumn (Froux et al., 2004; Hüve et al., 2006). Large increases of T_c can be induced by increasing ambient temperatures over a few days as shown in silver fir (Robakowski et al., 2002). Similarly, a 10 °C shift of T_c was observed in *Q. suber* when ambient temperature was increased from 10 to 40 °C (Ghoul et al., 2003).

Several studies showed that drought does also lead to an increase of thermostability of PSII. This was the case in *Ce-*

drus atlantica (Epron, 1997a; Ladjal et al., 2000). In *Q. suber*, a 10 °C increase of T_c was evidenced during the course of a severe drought that resulted in complete stomatal closure (Ghoul et al., 2003). The rate of increase of T_c was rather high (close to 1 °C day⁻¹) during the cited experiments. Unfortunately, the reversibility after re-irrigation of such large increases was never documented. The degree of reversibility of T_c acclimation would bring interesting information about the processes involved.

Changes of T_c reflect acclimation processes in the PS II reaction centers. T_c is much higher than the optimum temperature for light driven electron flux (T_{opt}) estimated from the temperature response of J_{max} , the maximal rate of electron flow derived from leaf photosynthesis models. T_{opt} is usually close to 35 °C (Dreyer et al., 2001; Medlyn et al., 2002a). T_{opt} has been shown to acclimate to some extent to long term changes in ambient temperature (Berry and Björkman, 1980; Medlyn et al., 2002b; Yamori et al., 2005). It remains nevertheless to be demonstrated whether increases in T_c are matched by increases of the thermal optimum of light driven electron flow (T_{opt}) and whether the two parameters display similar levels of acclimation to a rise in ambient temperature.

Large scale inter-specific or genotypic comparisons of T_c were only seldom conducted. The few available studies failed to reveal higher values in species from warmer environments (Knight and Ackerly, 2002). The open question are therefore: (i) whether genotypes or species from warm environments display larger values of T_c under common conditions of moderate ambient temperatures, and (ii) whether they differ in the ability to acclimate to increasing ambient temperatures by enhanced values of T_c ; in other words, whether they display a larger plasticity of T_c than those from cooler environments.

The present study therefore aimed at:

- (1) Checking whether an ambient temperature-induced increase in the critical temperature for photochemistry (T_c) recorded in the dark was matched by a similar increase in the optimal temperature for light driven electron transport (T_{opt}). T_{opt} was estimated from the response to air temperature of actual quantum yield of photochemistry of attached leaves under moderate irradiance and high CO₂.
- (2) Checking whether the ability of T_c to acclimate to moderately increasing temperatures, and the extent of this acclimation, was similar among oak species from different geographic areas (Mid-European vs. Mediterranean).
- (3) Checking whether the return to initial lower temperatures resulted in a reversal of the observed increases of T_c , and T_{opt} and to quantify this reversibility in the same oak species.

To answer these questions, we used saplings from five oak species (three Mediterranean and two mid European ones) grown under common conditions in a greenhouse in North-eastern France.

2. MATERIALS AND METHODS

2.1. Plant material

Acorns of cork oak (*Q. suber* L.), zeen oak (*Q. canariensis* Willd.) and kermes oak (*Q. coccifera* L.) were collected in Northern-Tunisia between Tabarka and Ain Drahem, during autumn 2003 and germinated in a greenhouse at INRA Nancy during spring 2004. Acorns of pedunculate (*Q. robur* L.) and sessile oak (*Q. petraea* Matt. Liebl.) were collected in the Domain Forest of Compiègne, Northern France during autumn 2003 and planted in the same greenhouse. Saplings were grown in 5L pots on a peat/sand mixture (1/2 v/v) and fertilised with a slow release fertiliser Nutricot 100 (N/P/K, 13/13/13 + oligoelements). Irrigation was automated. The experiments were conducted during October 2004.

2.2. Thermal preconditioning

During the experiments, 10 potted saplings of each species were transferred to a climate chamber under a PPFD of 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$, 60% relative humidity and air temperature controlled at 15, 25, or 35 °C, with a 14/8 h day/night photoperiod. The potted saplings were kept during one week successively at each temperature and returned to 15 °C. Measurements were conducted after 5 to 7 days acclimation to each ambient temperature, on fully expanded mature leaves produced during Spring 2004.

2.3. Maximal quantum yield of photochemistry (F_v/F_m) in leaves

Chlorophyll a fluorescence was measured with a modulated fluorimeter (PAM 2000, Heinz Walz, Effeltrich, Germany) on attached leaves that had been dark-acclimated for 8 h prior to harvest ($n = 6$). Ground fluorescence (F_0) was obtained with a low intensity modulated light (600 Hz, 650 nm, PFD < 1 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Maximal fluorescence (F_m) was induced by a saturating flash (halogen lamp, 0.8 s, 4500 $\mu\text{mol m}^{-2} \text{s}^{-1}$). The ratio F_v/F_m was used as an estimate of maximal quantum yield of photochemistry (Kitajima and Butler, 1975).

$$\frac{F_v}{F_m} = \frac{F_m - F_0}{F_m}$$

2.4. Temperature optimum of light-driven electron flow

The temperature optimum of light driven electron flow was assessed from the quantum yield of photochemistry ($\Delta F/F_m$, Genty et al., 1989). Saplings were transferred from the climate chamber to the laboratory, and one leaf inserted into a gas exchange chamber ADC (ADC Bioscientific, Herts, UK). The chamber was illuminated with a halogen lamp and incident photosynthetic photon flux density at leaf level (below the window) was set at 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The temperature in the chamber was controlled with water circulating in the aluminium body and through a water bath with temperature control. Leaf temperature was measured with a thermocouple at leaf contact, inserted through the bottom of the chamber, and recorded on a Campbell data recorder CR10X (Campbell Scientific, Logan, Utah, USA). Inflowing air was humidified and dew point temperature imposed through a home built water-trap to provide at least 50% RH

at the highest temperature. Inlet air was controlled at 1% O₂ and 1000 ppm CO₂, to saturate photosynthesis, inhibit photorespiration and minimise the impact of changes in stomatal conductance on CO₂ assimilation and consequently on electron transfer. Chlorophyll a fluorescence was recorded with a Mini PAM (Heinz Walz, Effeltrich, Germany) with the fiber optics installed above the leaf chamber at an angle of 45 °C to avoid shading of fractions of leaf area. A saturating flash at maximal intensity was delivered every second minute to record $\Delta F/F_m$ as an estimator of the quantum yield of photochemistry. Under these conditions, changes in $\Delta F/F_m$ were considered to reflect changes in maximal electron flux rate. Temperature in the chamber was increased from 10 to 50 °C at a pace of 1 °C min⁻¹ approx. The relationship between leaf temperature and $\Delta F/F_m$ was used to estimate the optimal temperature of electron transfer by fitting the following empirical model to the data (June et al., 2004):

$$J_{TL} = J_{T_{opt}} \times e^{-\frac{(T_L - T_{opt})^2}{\Omega}}$$

with: J_{TL} : quantum yield at actual leaf temperature;
 $J_{T_{opt}}$: maximal quantum yield at optimal leaf temperature;
 T_L : actual leaf temperature;
 T_{opt} : optimal leaf temperature;
 Ω : curvature factor.

2.5. Critical temperature for thermal stability of PSII

Photosystem II thermostability was estimated from critical temperature inducing a steep rise in ground fluorescence (T_c) (Bilger et al., 1984; Ivanov et al., 1992) as described in Robakowski et al., 2002. A leaf disk was punched out and inserted into a device that exposes the disk to a target temperature (± 0.1 °C) that gradually increases from 20 to 60 °C at a constant rate of 1 °C min⁻¹. Temperature control is reached with Peltier elements allowing fast heating and cooling of the aluminium body of the device. A detailed description of this device may be obtained from P. Gross (INRA, Nancy Research Centre, Champenoux, France; Gross@nancy.inra.fr). Ground fluorescence of the treated leaf disk was monitored continuously in complete darkness with a PAM-2000 fluorometer (Heinz Walz, Effeltrich, Germany) with fiberoptics inserted into the aluminium body just over the leaf sample (red modulated light, PFD < 1 $\mu\text{mol m}^{-2} \text{s}^{-1}$). T_c was estimated graphically from the fluorescence traces. Mean values from four different leaves were computed and compared by a repeated measurement ANOVA and a Tukey post-hoc test at $P < 0.05$.

3. RESULTS

Maximal quantum yield of dark adapted leaves (F_v/F_m) was around 0.81 in *Q. suber* and in *Q. canariensis* after a week at 15 °C. F_v/F_m remained stable despite the increase of ambient temperature up to 35 °C and declined slightly after returning to 15 °C, the decline being larger in *Q. canariensis* where a mean value of 0.76 was reached (Fig. 1).

The actual quantum yield of photochemistry ($\Delta F/F_m$) showed a clear rise with temperature with a maximum between 25 and 35 °C and a decrease above this optimum. These temperature response curves were affected by ambient temperatures and showed a visible shift of T_{opt} towards higher temperatures (Fig. 2). Adjusting the temperature response function

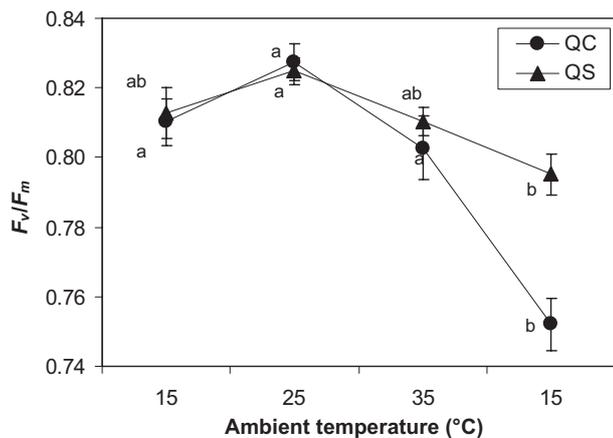


Figure 1. Effects of ambient temperature on the maximal quantum yield of photochemistry (F_v/F_m) in leaves of *Quercus suber* (QS) and *Q. canariensis* (QC). The ambient temperature sequence (5 days at each step) was 15, 25, 35 and back to 15 °C as shown by the lines between the individual points. Different letters indicate significant differences at $p < 0.05$ within a given species.

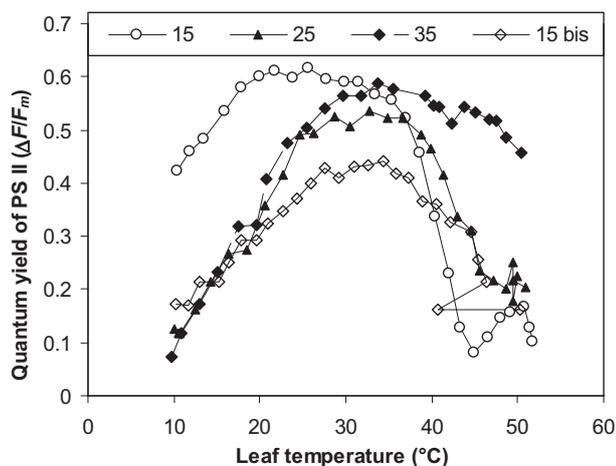


Figure 2. Examples of temperature response of PS II quantum yield measured by chlorophyll a fluorescence ($\Delta F/F_m$) under 1000 ppm CO_2 , 1% O_2 and a PFD of $500 \text{ mmol m}^{-2} \text{ s}^{-1}$ with leaves of *Q. canariensis* that were acclimated during 5 days to an ambient temperature of 15, 25, 35 and back to 15 °C (the latter referred to as 15bis in the legend). The response curves were used to estimate T_{opt} , the optimal temperature for light-driven electron flow with Equation (1). See text for details.

(Eq. (1)) to these responses yielded the estimates of T_{opt} used in the following analyses.

T_{opt} was 29.8 and 26.8 °C at 15 °C for *Q. suber* and *Q. canariensis*, respectively (Fig. 3A). T_{opt} increased significantly when ambient temperature was increased to 25 and 35 °C, to a different extent in the two species. The enhancement was much larger in *Q. suber* (+10.7) than in *Q. canariensis* (+1.9 °C). T_{opt} went on rising in *Q. canariensis* during reacclimation to 15 °C, while it decreased rapidly in *Q. suber*. The reversibility of the increase was not complete and T_{opt} remained largely

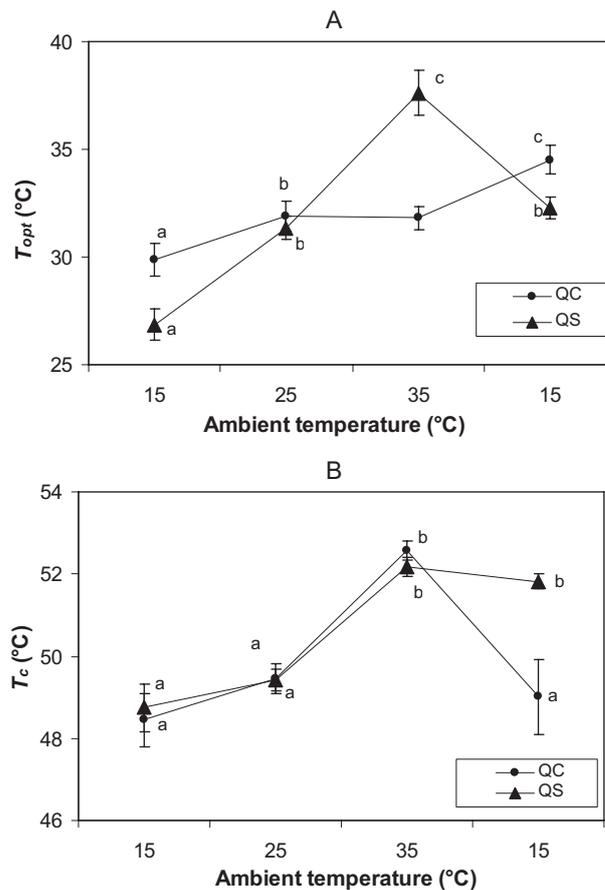


Figure 3. Effects of ambient temperature on (A) the optimal temperature of photochemical efficiency (T_{opt}) and (B) the critical temperature for PS II stability (T_c) of leaves of *Q. suber* (QS) and *Q. canariensis* (QC). The ambient temperature sequence (5 days at each step) was 15, 25, 35 and back to 15 °C as shown by the lines between the individual points. Different letters indicate significant differences at $p < 0.05$ within a given species.

above the initial values (+5.4 and 4.6 °C in *Q. suber* and *Q. canariensis*, respectively). T_c was initially very close in the two species (around 48 °C at 15 °C) and increased readily up to almost 52 °C at 35 °C ambient temperature (Fig. 3B). The decrease upon returning to 15 °C was stronger in *Q. canariensis* than in *Q. suber*. The correlation between the two values was very tight in the case of *Q. suber*, but not in *Q. canariensis* (Fig. 4).

A detailed comparison of T_c among species (Fig. 5) revealed a large and significant effect of ambient temperature and a smaller one of species, with no interaction (Fig. 5). The temperature rise induced significant increases of T_c , while the return to 15 °C resulted in a significant decrease without full recovery of initial values. Among species, only *Q. coccifera* differed from *Q. suber* but not from the other species. Initial values of critical temperature at 15 °C ambient temperature were comprised between 44.5 °C and 49.8 °C. At 35 °C, T_c increased to 50.8–52.5 °C with only small inter-specific

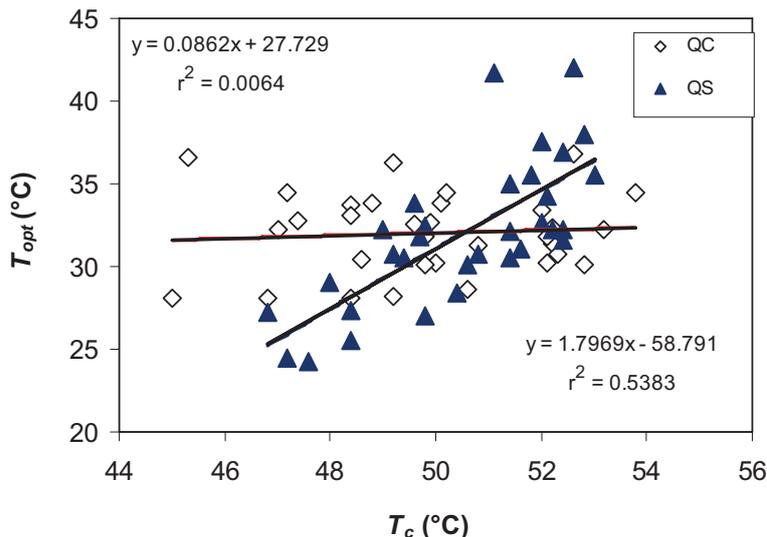


Figure 4. Correlation between critical temperature for PSII stability (T_c) and optimal temperature for light driven electron flow (T_{opt}). Each point represents a paired measurement of T_{opt} and T_c on a leaf and a disk from an adjacent leaf.

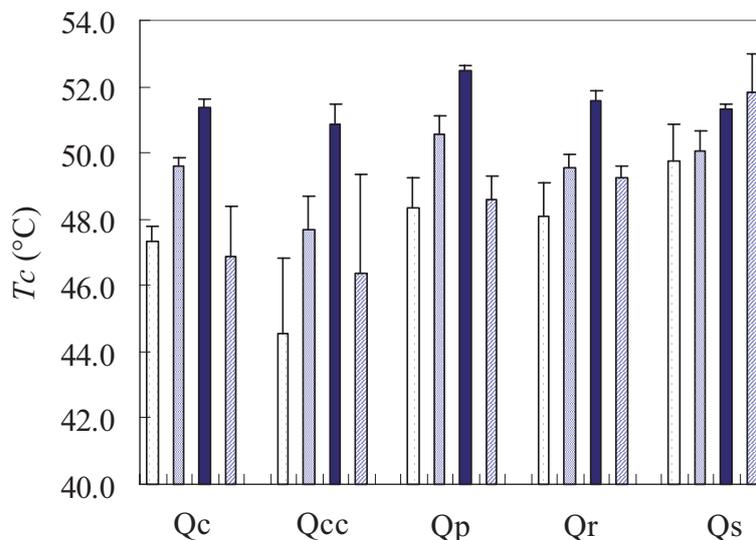


Figure 5. Effects of ambient temperature on the critical temperature for PS II stability (T_c) of leaves of *Q. suber* (Qs), *Q. canariensis* (Qc), *Q. robur* (Qr), *Q. petraea* (Qp) and *Q. coccifera* (Qcc). The ambient temperature sequence (5 days at each step) was 15, 25, 35 and back to 15 °C and resulting values of T_c are presented sequentially. Means \pm SE, $n = 4$. Results from a repeated measurements ANOVA were: species effect, $F = 5.67$, $p = 0.0073$; temperature effect: $F = 14.53$, $p < 0.0001$; interaction: $F = 1.28$, $p = 0.270$. Species differences were small and a post hoc Tukey test produced a difference between *Q. coccifera* and *Q. suber* ($p = 0.00759$), and small differences between *Q. coccifera* and *Q. petraea* ($p = 0.069$) and between *Q. canariensis* and *Q. suber* ($p = 0.0703$). All other comparisons resulted in $p > 0.01$. See Table I for detailed temperature effects.

differences. The recovery after return to 15 °C was very effective in all species except *Q. suber*.

4. DISCUSSION

The ambient temperatures imposed to the oaks saplings during this series of experiments (max 35 °C under moderate irradiance) never induced a severe decay of the photo-

synthetic apparatus, as shown by the almost complete stability of the maximal quantum yield of photochemistry (F_v/F_m). The thermal treatments therefore mainly induced acclimation (Sharkey, 2005). Nevertheless, a temperature of 35 °C was already at the threshold of damaging levels, as shown by the small decrease of F_v/F_m between 25 and 35 °C. Similar observations have been repeatedly reported. In *Q. suber*, F_v/F_m declined when ambient temperature increased above 32 °C Ghoul et al. (2003). This was also the case at 35 °C in

Table I. Effects of ambient temperature on the critical temperature for chlorophyll a fluorescence (T_c) of leaves of *Q. suber*, *Q. canariensis*, *Q. robur*, *Q. petraea* and *Q. coccifera*: pairwise comparisons of T_c at different acclimation temperatures with a Tukey post hoc test; probabilities are provided. Corresponding data in Figure 5.

Acclimation temperature (°C)	25	35	Back to 15
15	$p = 0.00848$	$p = 0.000166$	$P = 0.387$
25		$p = 0.0520$	$P = 0.296$
35			$P = 0.000526$

Acer pseudoplatanus, *Betula pendula*, *Fagus sylvatica* (Dreyer et al., 2001), in *Abies alba* (Robakowski et al., 2002) and in *Cedrus atlantica* and *C. libani* (Epron, 1997a). These decreases were mainly due to declining levels of maximal fluorescence (F_m) that may reach 65% at 45 °C for *Q. pubescens* (as compared to a 10% reduction in F_0) (Haldimann and Feller, 2004). Such a decrease in F_m is thought to result from a reversible change of the thermal dissipation rate constant K_D due to conformational changes in PSII allowing increased thermal energy dissipation (Yamane et al., 1997). Interestingly, when ambient temperature was returned to the initial level of 15 °C, F_v/F_m not only showed no sign of recovery, but even decreased further in the case of *Q. canariensis*. Such persistent after-effect of high ambient temperature remain poorly understood (Sharkey, 2005).

Severe damage to photosystems occurs only at much higher temperature, and is usually evidenced by a steep increase of ground fluorescence F_0 . In *Arbutus unedo*, such increases occurred above 47 °C (Schreiber and Berry, 1977). Similarly, F_0 was found to remain stable from 25 up to 45 °C in *Q. pubescens*, revealing a stability of the thylakoid membrane of PSII reaction centres till rather high temperatures (Haldimann and Feller, 2004). The increase of F_0 at high temperatures may be interpreted as a decrease of K_P , rate constant for photochemistry, due to fluidification of thylakoid membranes or to less efficient connections between light harvesting antenna and core reaction centres (Ducruet et al., 2007; Yamane et al., 1997).

T_c is known to be highly plastic. Increased T_c in response to rising temperature and to drought is a common occurrence in a many species. The largest acclimation described in the literature was recorded in *Q. suber*: T_c increased from 42 to 51 °C under drought at stable ambient temperatures (Ghouil et al., 2003). An almost similar increase was recorded when ambient temperatures increased from 15 to 35 °C. The increase observed in the five oak species was of smaller amplitude; this was due solely to the fact that initial values at 15 °C were larger in the present experiment while the highest levels under 35 °C ambient temperature were very similar (around 52 °C). This apparent discrepancy can be due to the fact that the saplings used by Ghouil et al. (2003) had been grown at low temperature before the measurements, while in the present case the saplings had already been submitted to summer temperatures as the measurements were made during October. This illustrates the plasticity of T_c , and the fact that minimal values of T_c

are only reached after long time at low temperatures, possibly with young leaves. This opens the question of the reversibility of the acclimation of T_c to high temperatures, which remains much less documented.

We found a large variability in the decrease of T_c after returning the saplings to 15 °C. In a majority of the tested species, returning to 15 °C resulted in a decrease of T_c down to values close to, but still slightly above the initial values. The decline of T_c was therefore almost of the same extent than the increase observed during the two preceding weeks. Only *Q. suber* did not display any down regulation after returning to 15 °C. To our knowledge, there are only few experimental data available on the reversibility of acclimation of T_c to high temperatures, and it is therefore still difficult to produce a clear conclusion about the general characteristics of the de-acclimation process.

Inter-specific differences of T_c were small, as well for the absolute values as for the degree of plasticity. Moreover, small differences were detected before the high temperature treatment, while all species reached values close to 52 °C after the treatment and a few days at 15 °C resulted in almost full recovery of the initial low levels. Only *Q. suber* behaved abnormally as compared to the four other species, and there was no obvious reason for this.

The increase of T_c was clearly paralleled by an increase in the optimal temperature for electron flow (T_{opt}). T_{opt} was as expected much smaller than T_c , and close to 26–30 °C in saplings at 15 °C. It increased to 35 °C in *Q. suber* and to lower values in *Q. canariensis* in response to moderate heat. In this latter species T_{opt} increased after returning to 15 °C, which could mean that the low values at 35 °C were an artefact. A direct comparison of T_c and T_{opt} revealed a relatively tight correlation in *Q. suber*: acclimation of T_c to increased ambient temperature has visible consequences for the optimal temperature for light-driven electron transfer. Such was not the case in *Q. canariensis*, for a reason that remains to be investigated.

A close link between the plastic responses of T_c and T_{opt} has important practical consequences, as T_c is very easy to record with automated procedures, while T_{opt} requires the use of a gas exchange chamber, calibrated gas mixtures and standardised conditions that make a large scale survey among species and genotypes time-consuming and unreliable. A new version of the measurement device developed in our laboratory can simultaneously process six leaf samples, and allows repetitions and quantitative analyses of diversity.

5. CONCLUSION

- (1) All tested oak species displayed a large plasticity of the critical temperature for photochemistry (T_c) with increasing ambient temperatures; the geographic origin of the species had no visible consequence for this plasticity, nor for the maximal value of T_c .
- (2) The increase of T_c was reversible in all tested oak species (with the notable exception of *Q. suber*); this rapid reversion lead to a return to close-to-initial values.

- (3) Increases in T_c were to some extent paralleled by changes in optimal temperature for electron transfer; the low number of available data allowed no clear conclusion about the respective amplitude of the changes; but the observed changes clearly show that changes in thermostability of reaction centres are not occurring independently of changes in the electron transport chain, and may be used as an index for an acclimation of the whole photosynthetic apparatus.

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