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Original article

Temperature response of photosynthesis of silver fir (*Abies alba* Mill.) seedlings

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Abstract – Temperature responses of photosynthesis were assessed in a shade tolerant tree species (silver fir, *Abies alba* Mill.) using leaf gas exchange and chlorophyll *a* fluorescence measurements. Four-year-old seedlings grown in a greenhouse in N-E France were transferred into a climate chamber and kept during 24 hours at six temperature levels: 10, 18, 26, 32, 36 and 40 °C. Response curves of net CO_2 assimilation to substomatal CO_2 partial pressure were obtained on small twigs bearing a single row of needles under saturating irradiance. Maximal carboxylation rate (V_{cmax}) and maximal light driven electron flow (J_{max}) were estimated by fitting Farquhar's model to the response curves at each temperature. "Dark" respiration (R_d) was estimated at the end of each response curve by measuring gas exchange after 5 min darkness in the chamber. The temperature responses of the three parameters were fitted to a thermodynamic model. Mean values at a reference temperature of 25 °C were 37, 91 and 2.6 µmol m^{-2} s^{-1} for V_{cmax}, J_{max} and R_d, respectively. Optimal temperature was higher for V_{cmax} (36.6 °C) than for J_{max} (33.3 °C), and no optimum was detected for R_d. Such values are very close to those of broadleaved tree species. The J_{max}/V_{cmax} ratio decreased with temperature. Activation energies were estimated at 56, 50 and 23 kJ mol^{-1} for V_{cmax}, J_{max} and R_d, respectively. The maximal quantum efficiency of PS II estimated from chlorophyll *a* fluorescence declined significantly above 36 °C. It nevertheless fully recovered after 1 day at 25 °C even after 24 h heat stress at 40 °C. Irreversible injuries to PS II revealed by severe increases of ground fluorescence occurred at about 47 °C. This critical temperature for PS II increased with the air temperature imposed during the night preceding the measurements.

maximal carboxylation rate / maximal light driven electron flow / dark respiration / optimal temperature / thermostability

Résumé – Réponse thermique de la photosynthèse de jeunes semis de sapin (*Abies alba* Mill.). La réponse à la température de la photosynthèse du sapin pectiné (*Abies alba*, conifère particulièrement tolérant à l'ombre) a été caractérisée en utilisant des mesures d'échanges gazeux foliaires et de fluorescence de la chlorophylle *a*. Des semis de quatre ans élevés dans des conteneurs et en serre dans le N-E de la France (INRA Nancy, Champenoux) ont été transportés dans une chambre climatisée et maintenus à 6 températures (10, 18, 26, 32, 36 et 40 °C) pendant 24 h. Des courbes de réponse de l'assimilation nette de CO_2 à la concentration intercellulaire de CO_2 ont été établies sous éclairement saturant sur des rameaux de l'année portant une seule couche d'aiguilles. La vitesse maximale de carboxylation (V_{cmax}) et le flux maximal d'électrons (J_{max}) ont été estimés pour chacune de ces courbes en ajustant les résultats expérimentaux au modèle de photosynthèse de Farquhar. La respiration des aiguilles (R_d) a été estimée après chaque courbe de réponse en mesurant les échanges gazeux après 5 min d'obscurité dans la chambre. Les valeurs moyennes des paramètres du modèle à 25 °C ont été estimées à 37, 91 et 2,6 µmol m^{-2} s^{-1} pour V_{cmax}, J_{max} et R_d, respectivement. L'optimum thermique était plus élevé pour V_{cmax} (36,6 °C) que pour J_{max} (33,3 °C), et aucun optimum n'a pu être estimé pour R_d. L'augmentation de la température conduisait à une diminution du rapport J_{max}/V_{cmax}. Les énergies d'activation ont été estimées à 56, 50 et 23 kJ mol^{-1} pour V_{cmax}, J_{max} et R_d, respectivement. Le rendement

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quantique maximal de la photochimie, estimé à l'aide de la fluorescence de la chlorophylle *a*, diminuait significativement au dessus de 36 °C. Ce rendement quantique a néanmoins récupéré pleinement après une journée à 25 °C, même après un stress thermique de 24 h à 40 °C. Des dommages irréversibles au photosystème II ont été détectés sous la forme d'une augmentation de la fluorescence de base au dessus de 47 °C. Cette température critique pour le PS II a fortement augmenté avec la température imposée la nuit précédente.

température optimale / vitesse maximale de carboxylation / flux maximal d'électrons / respiration / stabilité thermique

Abbreviations:
C_i – CO_2 substomatal concentration
F_0 – ground fluorescence
F_m – maximal fluorescence
F_v/F_m – maximal quantum efficiency of PS II photochemistry
J_{max} – maximal light driven electron flow
K_c, K_o– Michaelis-Menten constants of rubisco for CO_2 and O_2, respectively
PPFD – photosynthetic photon flux density
PS II – photosystem II
R_d – (dark) respiration due to phosphorylative oxidations
RuBP – ribulose bisphosphate
T_c – critical temperature for PS II
V_{cmax} – maximal carboxylation rate
τ – specificity factor of Rubisco.

1. INTRODUCTION

Decline of silver fir (*Abies alba* Mill.) stands is an important problem in Central European forests, and particularly in the Sudete mountains of southern Poland. The common sense states that the observed decline processes are not related to a single inducing factor, but that they reflect a generally low resistance and low adaptability of this species to adverse environmental factors, even within its natural distribution area. Recent observations of an abundant natural regeneration of this species in Carpathian Mountains suggest that recent reductions of air pollution in addition to local impact of global climate changes may have improved the fitness of this species (Korczyk, personal communication).

Temperature is a major environmental factor able to modulate growth and survival of silver fir. One of the basic processes governing productivity and growth that may be severely affected by temperature is carbon gain, i.e., photosynthesis and respiration. Optimal temperatures for net CO_2 assimilation are known to vary among species, and within species among provenances, displaying either a genetic variability related to the origin of the provenances [5, 6] or a phenotypic variability due to acclimation to different growth temperatures [24, 27]. As net assimilation results from a combination of several processes such as CO_2 diffusion from atmosphere to chloroplasts, carboxylation of RuBP, light driven electron flow, respiration, etc. there is a need to document the temperature response of these individual processes.

Leaf-level models of photosynthesis are useful in quantifying the response of individual photosynthetic processes to varying environmental conditions. Farquhar's [4] biochemically based model of leaf photosynthesis is often used to parameterise and compare photosynthetic capacity among individuals and genotypes. The key parameters describing leaf photosynthesis are the maximal rate of carboxylation (V_{cmax}), the maximal light driven electron flow (J_{max}) and the mitochondrial respiration due to phosphorylative oxidation (R_d) [4]. Some of the parameters used in the model, for example the CO_2/O_2 specificity of Rubisco, seem to be relatively stable among a vast group of plants. Others may considerably differ among species and such groups as dicots and monocots, hardwoods and conifers, and annuals and perennials [29].

Many studies provided estimates of V_{cmax}, J_{max}, and R_d and quantified the relationships between these parameters and the total amount of leaf nitrogen per unit leaf area for different tree species [14, 16, 20, 26]. However, there are only a few data sets on the temperature dependency of these parameters for trees, particularly for conifers. Recent results showed the occurrence of some degree of interspecific variability of the temperature responses of photosynthetic processes among broadleaved tree species [2]. It was therefore of importance to complete the already gathered data set by temperature responses of needle photosynthesis in silver fir. In this work, we determined V_{cmax}, J_{max}, and R_d and we studied their temperature response in silver fir (*Abies alba* Mill.) needles using Farquhar's model [9].

High temperatures are known also to affect the thermostability of photochemistry which may be studied using chlorophyll *a* fluorescence [10]. The quantum yield of photochemistry of dark adapted leaves (F_v/F_m) usually decreases steeply at temperatures close to 38 °C [2, 3, 10]. Ground fluorescence (F_0) increases at a critical temperature [1] that is usually much higher than the point

of decreasing F_v/F_m, i.e., above 45 ºC [2]. The rise of ground fluorescence is probably due to a separation of light harvesting complexes from the PS II core complexes or to a denaturation of PS II reaction centres [30]. The PS II critical temperature increases (i.e., thermostability of PS II increases) when leaves are pre-exposed to moderately elevated temperatures [12]. We therefore estimated the values of PS II critical temperature and assessed the potential acclimation in this parameter resulting from short term acclimation to high temperatures.

2. MATERIALS AND METHODS

2.1. Model

The temperature dependence of the parameters ($P_{(T)}$) of plant photosynthetic capacity can be described by an Arrhenius type exponential function [17, 23]. Temperature dependence of the specificity factor of rubisco (τ) and of the affinity for CO_2 and O_2 (K_c and K_o and R_d) are modelled with the following increasing function:

$$P_{(T)} = P_{(T_{ref})} \times e^{\left[\frac{\Delta H_a}{R \times T_{ref}} \times \left(1 - \frac{T_{ref}}{T}\right)\right]} \quad (1)$$

where $P_{(T_{ref})}$ is the parameter value at a reference temperature T_{ref} (298.16 K), ΔH_a (J mol^{-1}) is the activation energy, R (8.3143 J K^{-1} mol^{-1}) is the gas constant, and T (K) is the leaf temperature.

The temperature dependence of V_{cmax} and J_{max} is usually expressed with a model including an optimum [17, 28] as:

$$P_{(T)} = \frac{P_{(T_{ref})} \times e^{\left[\frac{\Delta H_a}{R \times T_{ref}} \times \left(1 - \frac{T_{ref}}{T}\right)\right]}}{1 + e^{\left[\frac{\Delta S \times T - \Delta H_d}{R \times T}\right]}} \times \left(1 + e^{\left[\frac{\Delta S \times T_{ref} - \Delta H_d}{R \times T_{ref}}\right]}\right) \quad (2)$$

where $P_{(T_{ref})}$ is the potential value that the parameter would have at the temperature T_{ref} in the absence of high temperature inhibition , ΔS (J K^{-1} mol^{-1}) is an entropy term, ΔH_d (J mol^{-1}) is the deactivation energy of the given parameter.

The optimal temperature is derived from this function as:

$$T_{opt} = \frac{-\Delta H_d}{R \times \ln\left(\frac{-\Delta H_a}{\Delta H_a - \Delta H_d}\right) - \Delta S} \quad (3)$$

The model primary data (K_c, K_0 and τ) were taken from Jordan and Ogren [13] and Von Caemmerer et al. [25]. Apparent quantum yield of electron flow was set at 0.24 [9]. The equations and statistical methods put together by Dreyer et al. [2] were used to describe the temperature dependence of the photosynthetic parameters and to compute values of optimal temperature.

2.2. Plant material

Seedlings of silver fir were grown from seeds collected from a selected tree in Midzygórze Forest Inspectorate (50º 15’ N, 16º 45’ E) in the Polish Sudety Mountains. The mother tree was at 620 m a.s.l., in southern exposure. Mean annual temperature at this site is 5.6 ºC, mean temperature of the coldest month (January) –4.3 ºC, mean temperature of the hottest month (July) + 15.1 ºC. Mean annual precipitation was estimated to be about 1030 mm.

The seedlings were grown in a nursery in Midzygórze for the first three years. During April 1999, they were put into polythene rolls with soil from the pots in which they had been growing and transported in plastic bags to a greenhouse at Champenoux (48º 44’ N, 6º 14’ E), near Nancy, France. There they were transplanted into seven-litres pots using a mixture of blond peat and sand (2/5 v/v). They were fertilised at the beginning of May with 10 g L^{-1} slow release fertiliser Nutricote 100 13/13/13 N/P/K (supplemented with oligoelements). Each seedling was watered to field capacity twice a day using drip irrigation. In the greenhouse, the mean daily temperature fluctuated between 19 and 32 ºC during the whole year, the relative air humidity remained at about 64%, and the mean daily PPFD values varied from 250 to 650 µmol m^{-2} s^{-1}. The trees were grown for one year under these conditions.

2.3. Temperature treatments

The potted seedlings were transferred during June 2000 to a climate chamber and acclimated during one week under following conditions: air temperature = 25 ºC, relative humidity = 70% and PPFD = 250 µmol m^{-2} s^{-1}. Thereafter, air temperature was changed in six 24 h steps (10, 18, 26, 32, 36, 40 ºC) while RH and PPFD were kept constant. The seedlings were exposed to each temperature for 24 hours prior to measurements.

2.4. Gas exchange measurements and model parametrization

Gas exchange was recorded on small twigs with a portable open gas exchange system LiCor 6400 (LiCor, Nebraska, USA) using a 6 cm^2 chamber with a red-blue illuminator. Silver fir needles grow on the twigs in two layers: the upper layer was severed to avoid self-shading among needles. A twig with one layer of needles was introduced into the photosynthesis chamber. The microclimate in the chamber was set at: leaf temperature close to external, RH at 65–70% and PPFD was at the saturating level of 1500 $\mu mol\ m^{-2}\ s^{-1}$. Photosynthesis of needles was induced during 25–30 minutes at ambient CO_2 (35 Pa) prior to generation of A/C_i curves. Afterwards the concentration of CO_2 was increased to 175 Pa and gradually reduced in 13 steps to 5 Pa. Each step comprised a stabilisation (at least 4 min) and three records at 1-min intervals of net assimilation rate (A), stomatal conductance to water vapour (g_s) and intercellular CO_2 mole fraction C_i. After the last step of each AC_i curve, the CO_2 concentration was changed to 40 Pa, the light in leaf chamber was shut down and the respiration due to oxidative phosphorylation ("dark respiration" – R_d) was measured after 5 min. in the dark. The needles in the gas exchange chamber were collected and their projected area was computed with a Delta T Area Meter (Delta T, Hoddesdon, United Kingdom). Measured projected area was used to recompute all gas exchange parameters. Values of V_{cmax} (maximal carboxylation rate) and J_{max} (maximal light driven electron flow) were estimated by fitting the model of Farquhar [4] to the Rubisco limited portion of the A/C_i curves at lower C_i (CO_2 substomatal concentration) and to the RuBP (ribulose bisphosphate) regeneration limited one at saturated level of C_i, respectively (for details on the procedure see [2, 15]).

2.5. Contribution of twigs to respiration

A separate experiment was conducted to estimate the relative contribution of needles, twigs and buds to "dark" respiration. R_d was measured on a leafy twig with buds, a leafless twig with buds, and without buds at a tissue temperature of 25 ºC in five seedlings in the dark. Needles, shoots and buds were dried in the oven and their dry mass was used as a basis to express R_d. The respiration of needles was calculated subtracting R_d of the leafless twig with buds from that of the leafy twig with buds. Likewise, the R_d of buds was estimated by subtracting R_d of the needles and of the leafless twig from the R_d of the leafy twig with buds. Specific respiration was computed as R_d/biomass.

2.6. Thermal stability of photochemistry

Chlorophyll *a* fluorescence (F_0 – ground fluorescence, F_m – maximal fluorescence) and the maximal quantum yield of PS II photochemistry (the ratio of variable to maximal fluorescence F_v/F_m, [7]) were recorded in needles of 5 silver fir seedlings prior to gas exchange measurements at the different temperatures. Five measurements were carried out per seedling at each temperature. The restoration of PS II function after exposure to 40 ºC was monitored during 3 days at 25 ºC. The plants were dark adapted for 12 hours on each day prior to measurements carried out with a portable modulated fluorometer MiniPAM (Walz, Effeltrich, Germany).

Thermotolerance of needle photochemistry and its ability to acclimate to increasing air temperature were estimated using the critical temperature for PS II photochemistry defined as the "thermal breakpoint" – the temperature at which F_0 exhibits an upward inflection [1, 18]. Needles were collected from seedlings and put into a moist filter paper. They were kept for two hours in the dark under ambient temperature (25 ºC) prior to measurements and introduced into a temperature-controlled aluminium body with the end of the fiberoptics of a fluorometer (PAM 2000, Walz, Effelrich, Germany). Ground fluorescence was induced with a red diode at a low PPFD of 1 $\mu mol\ m^{-2}\ s^{-1}$. The temperature of needles was gradually increased from 20 to 60 ºC at a rate of 1 ºC min^{-1}, F_0 was continuously recorded with a chart recorder and the critical temperature estimated graphically.

3. RESULTS

3.1. Temperature responses of needle photosynthesis

The values of V_{cmax} (maximal carboxylation rate) and J_{max} (maximal light driven electron flow) were estimated by fitting the Farquhar's model to the Rubisco limited portion of the A/C_i curves at low values of C_i (CO_2 substomatal concentration) and to the RuBP (ribulose bisphosphate) regeneration limited one at saturating level of C_i, respectively. Both phases of A/C_i curves were well marked at each temperature level, with clear

transitions from the first to the second. No decrease of net assimilation was recorded at over-saturating CO_2, indicating the absence of limitation due to triose phosphate utilization (starch and sucrose production [9, 22]).

The temperature response functions normalised to values at 25 °C are displayed in *figure 1a*. Both V_{cmax} and J_{max} displayed marked increases with temperature, followed by visible decreases at 40 °C. This enabled us to estimate the optimal temperature (36.6 and 33.3 for V_{cmax} and $J_{max,}$ respectively). The ratio J_{max}/V_{cmax} decreased with temperature from 2.9 at 10 °C to 1.1 at 40 °C (*figure 1b*). The values of activation and deactivation energy as well as of entropy factor obtained by adjusting an Arrhenius function (Eq. (2)) on the temperature response of V_{cmax} and J_{max} are displayed in *table I*.

The measured values of shoot R_d increased exponentially with temperature, although with more scatter in the data (*figure 1c*). Computed values of R_d at 25 °C and of activation energy for R_d are displayed in *table I*. This response was a composite of needle, bud and twig respiration. An estimate of the mean contribution of each of these compartments to the overall CO_2 release by the shoot is displayed in *table II*; around 33% of the CO_2 released in the measurement chamber originated from the needles. The contribution of twigs and buds to measured gas exchange was therefore not negligible, and the likely estimate of needle respiration at 25 °C was closer to 0.86 µmol m^{-2} s^{-1}. Interestingly, specific respiration of twigs and buds was larger than that of needles (*table II*).

Table I. Means (± SE when it could be calculated) of the parameters describing temperature responses of needle photosynthetic capacity in 4-year-old seedlings of silver fir (*Abies alba* Mill.). V_{cmax} – maximal rate of carboxylation, J_{max} – maximal rate of electron flow, R_d – dark respiration, ΔH_a – activation energy, ΔH_d – deactivation energy, ΔS – entropy factor, T_{opt} – optimal temperature.

Parameters	V_{cmax}	J_{max}	twig R_d	needle R_d
Value at 25 °C (µmol m^{-2} s^{-1})	37.3 ± 3.4	91.1 ± 6.4	2.62 ± 0.3	0.86
T_{opt} (°C)	36.6 ± 1.9	33.3 ± 1.4		
ΔH_a (kJ Mol^{-1})	56.2 ± 8.4	50.3 ± 7.8	22.6 ± 3.3	
ΔH_d (kJ Mol^{-1})	272	217		
ΔS (J K^{-1} Mol^{-1})	867	697		

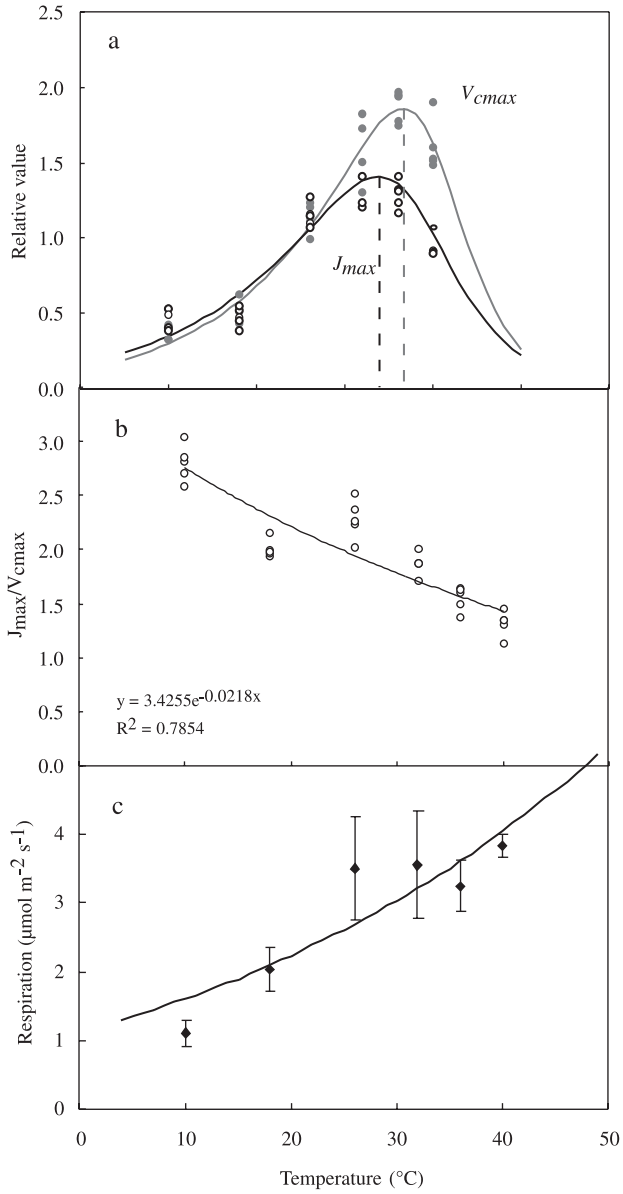

Figure 1. (a) Temperature responses of maximal rate of carboxylation (V_{cmax}) and of maximal light driven electron flow (J_{max}). V_{cmax} and J_{max} estimated at six different temperatures and normalized to the mean value at 25 °C in needles from five 4-year-old seedlings of *Abies alba* (n = 5). The values of V_{cmax} and J_{max} were estimated by fitting the response functions to curves of net CO_2 assimilation rate (A) to substomatal CO_2 partial pressure (C_i) obtained at 6 different temperatures. (b) Temperature response of the ratio J_{max}/V_{cmax} (actual values). (c) Temperature response of "dark" respiration of needles and twigs (mean ± SD, Arrhenius function adjusted to the data, see *table I* for coefficients).

Table II. Mean values (± SD) of specific dark respiration (R_d) of needles, buds and bare shoot in one year old silver fir twigs, and weighted contribution of each compartment to total twig respiration (n = 5).

Organs	R_d ± SD (nmol g^{-1} s^{-1})	Min – Max (nmol g^{-1} s^{-1})	Weighted contribution to twig respiration
Needles	3.7 ± 1	2 – 5	0.33 ± 0.12
Buds	5.6 ± 2	4 – 8	0.23 ± 0.10
Twig	8.1 ± 2	6 – 11	0.44 ± 0.05
Total	17.4 ± 3		1.00

3.2. Photochemical efficiency and thermostability of PS II

Maximal quantum yield of PS II was 0.786 at 10 °C, and then increased with rising temperature to maximal value of 0.83 at 26 °C. Temperatures above 36 °C resulted in a decrease down to 0.71 at 40 °C (*figure 2*). Following the 2 days at 36 and 40 °C, the restoration of PS II efficiency occurred readily after 24 hours at 25 °C but was not complete (0.809 vs. 0.827 before the thermal treatment, $p < 0.001$; *figure 3*).

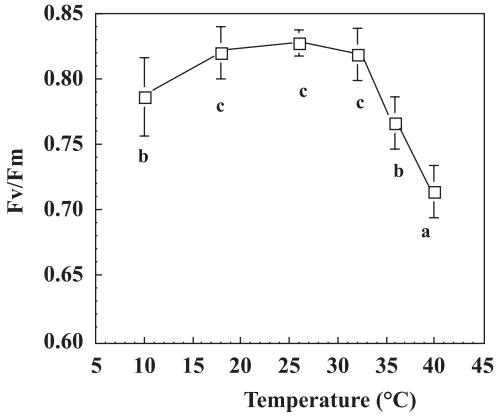

Figure 2. Temperature response of the maximal quantum efficiency of PS II (F_v/F_m) of silver fir needles (mean ± SD; n = 5). The seedlings were successively acclimated during 24 h to 6 levels of air temperature (10, 18, 26, 32, 36 and 40 °C) and F_v/F_m measured after 12 h darkness. Statistically significant differences among mean values were marked with different letters according to Tukey's a posteriori test with global α = 0.05.

The critical temperature for PS II stability in silver fir needles was close to 47 °C in needles acclimated to 10 °C. It increased steadily with acclimation temperature imposed during 24 h before the measurements by more than 4 °C (*figure 4*).

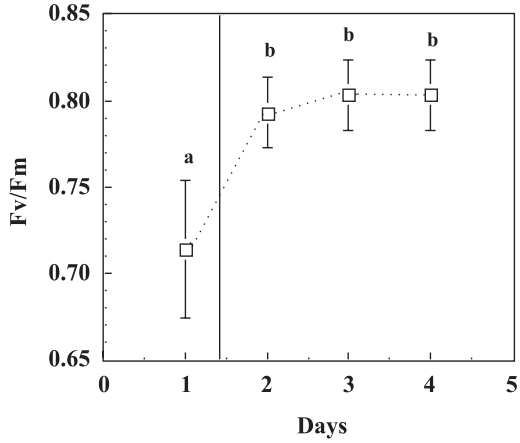

Figure 3. Recovery time course of maximal quantum efficiency of PS II (F_v/F_m, mean ± SD, n = 5) of silver fir needles after 24 h at 40 °C. Temperature was switched from 40 to 25 °C as indicated by the vertical bar. Statistically significant differences among mean values were marked with different letters according to Tukey's a posteriori test with global α = 0.05.

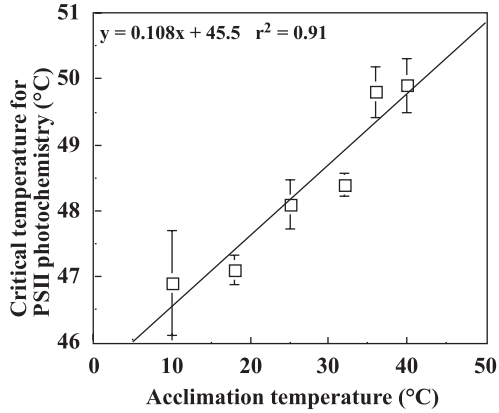

Figure 4. Impact of increasing acclimation temperature on the critical temperature for PS II photochemistry of silver fir needles (mean ± SD, n = 5). Critical temperature was estimated from the break point in the ground level fluorescence of needles submitted to a temperature increase of 1 °C min^{-1}. Acclimation time was 24 h for each temperature step.

4. DISCUSSION

Wullschleger [29] listed values of maximal carboxylation rates (V_{cmax}) and of light driven electron flow (J_{max}) among which only 10 had been measured on conifer species. Mean values for conifers were 25 μmol m^{-2} s^{-1} (range from 6 to 46, for V_{cmax}) and 40 μmol m^{-2} s^{-1} (17–121, for J_{max}). The large range of values was a result of species characteristics and of different experimental conditions (leaf temperature, light microlimate). Our estimates of V_{cmax} and J_{max} at 25 °C for *Abies alba* Mill. (37 and 91 μmol m^{-2} s^{-1}, respectively) were close to the highest among those reported for conifers. They are close to those of 2-year needles of adult trees from the fast growing *Pinus pinaster* [21], or of fertilised seedlings from the same species [19]. Such high values for a rather slow growing species may be explained by the high level of nutrients supplied in the potting medium as compared to natural conditions.

The temperature responses of V_{cmax} and J_{max} of silver fir displayed features that are common to those obtained with potted seedlings from a range of broadleaved species (higher temperature optimum for V_{cmax} than for J_{max}, decrease with increasing temperature of the ratio J_{max}/V_{cmax}, higher activation energy (ΔH_a), deactivation energy (ΔH_d) and entropy factor (ΔS) for V_{cmax} than for J_{max}) [2]. Nevertheless, optimal temperatures of V_{cmax} (36.6 °C) and J_{max} (33.3 °C) of silver fir were in the lowest range of the values recorded in broadleaved species, close to those of *Acer pseudoplatanus* and *Fagus sylvatica*. Values of activation energy of the two parameters V_{cmax} and J_{max} were also among the lowest ones.

Respiration of the leafy twigs was rather high on a needle area basis; after correction for the contribution of buds and stem, estimates yielded rather low values (around 0.9 μmol m^{-2} s^{-1}) which is much lower than those recorded in broadleaves. Similarly, the activation energy was close to the lowest ones recorded on broadleaved trees [2]. It is not known whether thermal sensitivities of respiration of different organs like buds, stems and needles, differ significantly.

The maximal quantum yield of *Abies alba* PS II (F_v/F_m) significantly decreased at temperatures above 36 °C, very similarly to what was observed with many other species (*Cedrus atlantica*, [3], *Juglans regia*, *Fagus sylvatica* and *Betula pendula* [2]), but at lower temperatures. This difference may presumably be explained by an adaptation to lower temperatures of *Abies alba*, a species typically occurring at higher altitudes in the mountains. The seedlings used in our experiment originated from 620 m a.s.l.

The temperature at which a rise of F_0 occurs is related to the critical temperature (T_c) irreversibly injuring the photosynthetic apparatus [1, 8]. The critical temperature recorded in silver fir needles increased to a large extent with the temperature experienced during the 24 h period before measurements, as was also noticed in a wide range of other species [10, 11]. The absolute levels recorded in our experiment were very close to those recorded on a range of broadleaved species acclimated to 20 °C [2].

As a conclusion, temperature responses of photosynthesis components in silver fir were very similar to those recorded with other tree species. Growth at high altitude probably does not exert a selective pressure on genotypes towards lower temperature optima for photosynthetic processes, or to particular performance of photosynthesis with respect to high temperatures. This lack of genotypic effect on absolute temperature responses expressed at a common microclimate does not exclude that species or genotypes growing at high elevations may exhibit different acclimation responses (in particular a potentially lower optimum for light driven electron transfer [20]). Further studies would be needed to document this point.

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REFERENCES

[1] Bilger H.W., Schreiber U., Lange O.L., Determination of leaf heat resistance: comparative investigation of chlorophyll fluorescence changes and tissue necrosis methods, Oecologia 63 (1984) 256–262.

[2] Dreyer E., Le Roux X., Montpied P., Daudet F.A., Masson F., Temperature response of leaf photosynthetic capacity in seedlings from seven temperate tree species, Tree Physiol. 21 (2001) 223–232.

[3] Epron D., Effects of drought on photosynthesis and on the thermotolerance of photosystem II in seedlings of cedar (*Cedrus atlantica* and *C. libani*), J. Exp. Bot. 48 (1997) 1835–1841.

[4] Farquhar G.D., Von Caemmerer S., Berry J.A., A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species, Planta 149 (1980) 78–80.

[5] Ferrar P.J., Slatyer R.O., Vranjic J.A., Photosynthetic temperature acclimation in *Eucalyptus* species from diverse

habitats, and a comparison with *Nerium oleander*, Aust. J. Plant Physiol. 16 (1989).

[6] Fryer J.H., Ledig F.T., Microevolution of the photosynthetic temperature optimum in relation to the elevational complex gradient, Can. J. Bot 50 (1972) 1231–1235.

[7] Genty B., Briantais J.M., Baker N.R., The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence, Biochim. Biophys. Acta 990 (1989) 87–92.

[8] Georgieva K., Yordanov I., Temperature dependence of chlorophyll fluorescence parameters of pea seedlings, J. Plant Physiol. 142 (1993) 151–155.

[9] Harley P.C., Tenhunen J.D., Modeling the photosynthetic response of C3 leaves to environmental factors, in: Modeling crop photosynthesis, from Biochemistry to Canopy, American Society of Agronomy and Crop Science Society of America, Madison, USA, 1991, pp. 17–39.

[10] Havaux M., Rapid photosynthetic adaptation to heat stress triggered in potato leaves by moderately elevated temperatures, Plant Cell. Environ. 16 (1993) 461–467.

[11] Havaux M., Tardy F., Temperature-dependent ajustement of the thermal stability of photosystem II in vivo: possible involvement of xanthophyll-cycle pigments, Planta 198 (1996) 324–333.

[12] Havaux M., Tardy F., Ravenel J., Chanu D., Parot P., Thylakoid membrane stability to heat stress studied by flash spectroscopic measurement of the electochromic shift in intact potato leaves: influence of the xanthophyll content, Plant Cell. Environ. 19 (1996) 1359–1368.

[13] Jordan D.B., Ögren W.L., The CO_2/O_2 specificity of ribulose 1,5-bisphosphate carboxylase/opxygenase. Dependence on ribulose bisphosphate concentration, pH and temperature, Planta 161 (1984) 308–313.

[14] Le Roux X., Grand S., Daudet F.A., Dreyer E., Le Dizes S., Parametrization and testing of a biochemically based photosynthesis model for walnut (*Juglans regia* L.) mature trees and seedlings, Tree Physiol. 19 (1999) 481–492.

[15] Le Roux X., Grand S., Dreyer E., Daudet F.A., Parametrization and testing of a biochemically based photosynthesis model for walnut trees (*Juglans regia*) and seedlings, Tree Physiol. 19 (1999) 481–492.

[16] Le Roux X., Walcroft A.S., Daudet F.A., Sinoquet H., Chaves M.M., Rodrigues A., Osorio L., Photosynthetic light acclimation in peach leaves: importance of changes in mass: area ratio, nitrogen concentration, and leaf nitrogen partitioning, Tree Physiol. 21 (2001) 377–386.

[17] Leuning R., Scaling to a common temperature improves the correlation between the photosynthetic parameters J_{max} and V_{cmax}, J. Exp. Bot. 48 (1997) 345–347.

[18] Logan B.A., Monson R.K., Thermotolerance of leaf discs from four isoprene-emitting species is not enhanced by exposure to exogenous isoprene, Plant Physiol. 120 (1999) 821–825.

[19] Loustau D., Ben Brahim M., Gaudillère J.P., Dreyer E., Photosynthetic response of two-year old Maritime Pine seedlings to Phosphorus nutrition, Tree Physiol. 19 (1999) 707–715.

[20] Niinemets U., Tenhunen J.D., A model separating leaf structural and physiological effects on carbon gain along light gradients for the shade tolerany species *Acer saccharum*, Plant Cell. Environ. (1997) 845–866.

[21] Porté A., Loustau D., Variability of the photosynthetic characteristics of mature needles within the crown of a 25-year-old *Pinus pinaster*, Tree Physiol. 18 (1998) 223–232.

[22] Sharkey T.D., Stitt M., Heineke D., Gerhard R., Raschke T.K., Heldt H.W., Limitation of photosynthesis by carbon metabolism. O_2-insensitive CO_2 uptake results from limitation of triose phosphate utilization, Plant Physiol. 81 (1986) 1123–1129.

[23] Sharpe P.J.H., DeMichele D.W., Reaction kinetics of poikilotherm development, J. Theor. Biol. 64 (1977) 649–670.

[24] Tjoelker M.G., Oleksyn J., Reich P.B., Seedlings of five boreal tree species differ in acclimation of net photosynthesis to elevated CO_2 and temperature, Tree Physiol. 18 (1998) 715–726.

[25] Von Caemmerer S., Evans J.R., Hudson G.S., Andrews T.J., The kinetics of ribulose-1,5-bisphosphate carboxylase/oxygenase in vivo inferred from measurements of photosynthesis in leaves of transgenic tobacco, Planta 195 (1994) 88–97.

[26] Walcroft A.S., Whitehead D., Silvester W.B., F.M. K., The response of photosynthetic model parameters to temperature and nitrogen concentration in *Pinus radiata*, Plant Cell. Environ. 20 (1997) 1338–1348.

[27] Wang K., Kellomaki S., Laitinen K., Acclimation of photosynthetic parameters in Scots pine after three years exposure to elevated temperature and CO_2, Agric. For. Meteorol. 82 (1996) 195–217.

[28] Wohlfarht G., Bahn M., Horak I., Tappeiner U., Cernusca A., A nitrogen sensitive model of leaf CO_2 and water vapour gas exchange: application to 13 key species from differently managed mountain grassland ecosystems, Ecol. Model. 113 (1998) 179–199.

[29] Wullschleger S.D., Biochemical limitations to carbon assimilation in C_3 plants– A retrospective analysis of the A/C_i curves from 109 species, J. Exp. Bot. 44 (1993) 907–920.

[30] Yamane Y., Kashino Y., Koike H., Satoh K., Increase in the fluorescence Fo level and reversible inhibition of Photosytem II reaction center by high temperature treatments in higher plants, Photosynth. Res. 52 (1997) 57–64.