European Journal of Forest Research (2019) 138:79–92
https://doi.org/10.1007/s10342-018-1155-7

ORIGINAL PAPER

Variation in the performance and thermostability of photosystem II in European beech (*Fagus sylvatica* L.) provenances is influenced more by acclimation than by adaptation

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Received: 7 May 2018 / Revised: 7 November 2018 / Accepted: 26 November 2018 / Published online: 8 December 2018

Abstract

The assisted migration of resistant seeds and seedlings may be a key to mitigating the effects of climate change on the productivity and composition of forest ecosystems. These efforts require an understanding of the intraspecific variability in the response of trees to extreme weather events such as heat waves. In this study, we assessed the geographical patterns of photosystem II (PSII) performance and thermostability in European beech (*Fagus sylvatica* L.) and whether intraspecific differences are associated with climate of origin. Two provenance trials with starkly contrasting climates were used for this study. Leaves were sampled both before and after natural heat stress exposure. Rapid chlorophyll fluorescence kinetics was used to evaluate PSII performance and PSII thermostability after simulated heat stress. The performance of PSII at 30 °C, which is still considered a non-damaging temperature, was generally slightly better at the warmer location than at the colder location. The populations originating closer to the Slovenian refugium, as well as those growing closer to their site of origin, showed better performance of PSII but not greater thermostability. The effect of simulated heat stress was much stronger in the colder plots compared to the warmer plots, but only for previously stressed trees. Likewise, we found indicators of geographical patterns of thermotolerance as well as relationships between thermotolerance and climate of origin mostly for trees exposed to natural heat. While the origin of provenances partly explained the variation among provenances, acclimation driven by climate played a major role in the response to heat stress. In beech, PSII seems to have a potential for coping with high temperature.

Keywords Heat stress · Thermotolerance · *Fagus sylvatica* L. · Chlorophyll *a* fluorescence · JIP test · Provenance trial · Intraspecific variability

Abbreviations

F_0	Basal fluorescence
F_v/F_m	Maximum quantum yield of PSII photochemistry
PI	Photosynthetic performance index

Communicated by Lluís Coll.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10342-018-1155-7) contains supplementary material, which is available to authorized users.

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R	Severity of thermal stress, the ratio between the F_v/F_m measured after simulated heat stress and the value of F_v/F_m measured under non-stressing temperature
T_{15}	The temperature at which F_v/F_m declines 15% from the maximum value
T_c	The critical temperature inducing abrupt changes in F_0

Introduction

Drought and heat waves are among the most important consequences of ongoing climate change. According to the 5th Assessment Report of the IPCC, "It is virtually certain that there will be more frequent hot and fewer cold temperature extremes over most land areas on daily and seasonal timescales, as global mean surface temperature increases. It is very likely that heat waves will occur with a higher frequency and longer duration (Pachauri and Mayer 2014)". During the summers 2014 and 2015, the whole of Central Europe suffered from at least three waves of extreme heats lasting more than 1 week, with daily maximum temperatures reaching up to 40 °C (Slovak Hydrometeorological Institute; http://www.shmu.sk/sk/?page=2049&id=643). Such reports refer to measurements in the shade 2 m above the soil surface; the actual temperature of directly irradiated surfaces such as sunny leaves may be substantially higher.

As heat is often associated with drought, high temperatures may easily reach or exceed the threshold of damage to physiological processes, because stomatal closure limits the ability of plants to avoid heat stress by transpiration-mediated cooling. Increases in temperature along with unchanged amounts of precipitation lead to significantly reduced growth and changes in the competitive ability of beech trees, especially at the xeric distribution border due to the exacerbating effects of heat on drought (Jump et al. 2006; Ježík et al. 2011).

Within the photosynthetic apparatus, photosystem II (PSII) is highly susceptible to overheating. Measurements of chlorophyll *a* fluorescence are therefore often used for assessing the impact of climate change on forest ecosystems (Bussotti et al. 2010; Bussotti and Pollastrini 2017). The fluorescence induction curve (FIC) changes under heat stress, with several indicators of overheating: (i) basal fluorescence (F_0) abruptly increases, which represents an accumulation of reduced quinone Q_A as a result of heat-induced inhibition of electron transport from Q_A to Q_B (Kouřil et al. 2004); (ii) maximal fluorescence (F_m) decreases, which represents the denaturation of chlorophyll proteins (Yamane et al. 1997); and (iii) a new *K*-peak appears in the FIC at approximately 0.3 ms. The *K*-peak indicates irreversible heat-induced damage to PSII, by inhibition of the oxygen-evolving complex, modification of light harvesting complexes or inhibition of electron transport from pheophytin to Q_A (Guissé et al. 1995; Lazár et al. 1997; Lazár and Ilík 1997).

The combined effects of environmental constraints may lead to higher sensitivity to heat stress (Digrado et al. 2017). Moreover, the combination of moderately high temperature and light inhibits the repair of PSII (Murata et al. 2007). On the other hand, antagonistic effects of environmental stresses on plants occur, where one constraint increases the tolerance of PSII towards another constraint. Generally, prior exposure to various stresses, e.g. moderate heat (Havaux 1993; Lazár et al. 1997; Ilík et al. 2018), light (Havaux et al. 1991) or drought (Snider et al. 2013), increases the thermotolerance of PSII. Drought increases the thermotolerance of PSII even before stomata are closed, so improved tolerance is not an indirect result of overheating that results from reduced transpiration (Ladjal et al. 2000). Under field conditions, this phenomenon may lead to various trade-offs, as heat stress is typically associated with drought and strong insolation. Consequently, PSII thermostability may exhibit fluctuations depending on external factors.

Plants have evolved various molecular and structural features to protect the photosynthetic apparatus from damage resulting from heat stress, representing both long-term adaptations and short-term adjustments to elevated temperatures (Berry and Bjorkman 1980; Havaux 1993) and indicating a broad acclimation potential of PSII in agricultural plant and tree species. Differences in heat tolerance among tree species are well documented (Dreyer et al. 2001; Froux et al. 2004); however, little is known about intraspecies genotypic and genetic variation. Experiments on conifers have demonstrated differences in photochemical efficiency under heat stress among spruce open-pollinated families (Bigras 2000), cedar, black pine, Aleppo pine and cypress seedlings (Froux et al. 2004). However, such differences have not yet provided evidence that the variation in PSII thermotolerance is associated with fitness. Association of physiological traits with climate or other environmental factors would be potential evidence of adaptation. Some studies have confirmed different physiological responses of beech provenances to environmental conditions depending on the altitude (Pšidová et al. 2018) or climate of origin (Robson et al. 2012; Hajek et al. 2016; Kučerová et al. 2018).

The most frequently proposed solution for mitigating climate change in the case of forest trees is assisted migration, i.e. the transfer of seeds or seedlings from heat- and drought-adapted populations in regions currently experiencing a climate that is equivalent to that expected at target sites in the future (Williams and Dumroese 2013). Such measures require knowledge of the geographical patterns of the adaptive features of tree populations, including thermostability of the photosynthetic apparatus (Konôpková et al. 2018). Therefore, our study focuses on the performance and thermostability of PSII variation among provenances of European beech (*Fagus sylvatica* L.), the most economically and ecologically important broadleaf species in Europe.

We intended to distinguish between the effects of adaptation and those of migration by comparing the correlation patterns of PSII performance and thermotolerance with the distance from the site of origin to the site of plantation and to the putative location of glacial refugia, respectively. Our next objective was to determine whether there are climatic and geographical patterns of PSII thermostability across the distribution range of beech in two provenance trials. We expected similar climatic trends of heat resistance among provenances (based on their origin) within both plots. Higher overall tolerance to heat stress for the warmer plot was assumed compared with those plants not acclimated to extremely high temperatures occurring more frequently during the vegetation season. To evaluate interannual shifts, we measured performance and responses of PSII to simulated acute heat stress both before and after a natural heat period (in June and July). We hypothesized that plants experiencing stress imposed by hot weather during the middle of the vegetation season would show more pronounced differences in response to simulated heat stress between plots than plants experiencing stress at the beginning of the vegetation season.

Materials and methods

Experimental material

The material used in this study was collected from two trial plots (Slovak and Czech) of a common garden experiment (provenance trial) established under the auspices of the Institute of Forest Genetics, Federal Forest Research Centre in Grosshansdorf, Germany. The complete experiment comprises a total of 23 trials and 70 tested populations of different origins (provenances). Seeds for the experiment were sown in 1996 in a common nursery; 2-year-old seedlings were subsequently transplanted throughout the trial plots. Both provenance tests were established under a randomized complete block design with three blocks; each plot initially contained 50 plants planted at 2×1-m spacing. Details regarding the design of the trials were summarized by Robson et al. (2018).

In the colder Slovak trial, located at Tále near the town of Zvolen, central Slovakia (48°38′N, 19°02′E, 810 m a.s.l.), 18 provenances were used, which encompassed most of the distribution range of beech in Europe. In the warmer Czech trial, which was located close to Zbraslav near Prague (49°57′N, 14°22′E, 360 m a.s.l.), a subset of ten provenances (planted in both trials) was sampled. The sites are climatically quite contrasting; the plot at Tále is located slightly above the beech climatic optimum, and the plot at Zbraslav is situated below the natural limit of beech distribution (Table 1). Sampling of mature leaves was performed in the summer (7 July 2013 and 10 July 2014) and in the early summer before the trees were exposed to natural heat stress (27 June 2016 and 15 June 2016) at Tále and Zbraslav, respectively (Table 2). Three trees per block and provenance were sampled from two blocks at each site. At Tále, a portion of block 3 turned out to have exceedingly wet soil, while at Zbraslav, block 3 was displaced and suffered high mortality. At both sites, sampling was therefore performed in only two blocks. Tree height at both sites reached up to 8.5 m and 10.5 m in 2013 and 2016, respectively. Leaf collection was accomplished during the early morning in order to avoid excessive insolation or temperature. Sun-exposed branches from the west-oriented upper third of the crown were collected and packed into plastic bags, which were put into a transportable refrigerator cooled to 5 °C to avoid dehydration or overheating during the transport to the laboratory. The leaves were subsequently exposed to acute heat stress simulated by a water bath.

Climatic characteristics were retrieved from the common database maintained at the Institute of Forest Genetics in Grosshansdorf. They are mostly derived from the WorldClim model with a 30 arc-second resolution (Hijmans et al. 2005) and were adjusted by local climatic models whenever possible. In addition to temperature and precipitation averages during the year and during the vegetation season, we used several bioclimatic indices. As our study focuses on heat stress, we included bioclimatic indices reflecting high temperatures: BIO4 = temperature seasonality; BIO5 = maximum temperature of the warmest month; BIO7 = annual temperature range; BIO8 = mean temperature of the wettest quarter; BIO10 = mean temperature of the warmest quarter; and BIO18 = precipitation of the warmest quarter. In addition, we calculated the maximum temperature of the warmest month and the Ellenberg quotient as EQ = the mean temperature of the warmest month/annual precipitation × 1000 (a measure of continentality and a good indicator of the beech distribution range, cf. Mátyás et al. 2010). The complete climatic data are presented in Suppl. 1a.

Assessment of the photosynthetic performance and thermostability of photosystem II

A WNE22 water bath (Memmert, Germany) was used to generate different water temperatures ranging from 30 to 48 °C (steps of 3 °C); for sampling in 2016, during early summer, the upper limit was 51 °C, as the response to high temperature was less pronounced compared to those of the measurements performed during July. The leaves were kept in enclosed Erlenmeyer flasks, and the flasks were put into the water bath at the appropriate temperature for 30 min. To assess the temperature conditions within flasks more

Table 1 Location and basic climatic characteristics of the European beech provenances and trial sites

No.	Location	Country	*T*	*Z*	Longitude	Latitude	Altitude	T_{mean}	$T_{5–9}$	P_{year}	$P_{5–9}$	EQ
Provenances												
3	Retz	F	x		3°06′	49°15′	140	9.99	15.84	641	283	27.6
4	Lagast	F	x	x	2°35′	44°09′	850	10.83	16.80	804	344	23.8
5	Fouger	F	x		1°09′	48°22′	180	10.02	15.70	670	271	26.4
12	Gruenewald	LUX	x	x	6°12′	49°40′	400	8.60	14.92	866	365	19.7
15	Elspeet	NL	x		5°48′	52°17′	33	8.97	14.68	799	353	20.5
17	Westfield	GB	x	x	− 3°25′	57°40′	10	8.23	12.70	671	303	21.8
23	Torup	S	x	x	13°12′	55°34′	40	7.90	14.38	640	286	25.9
26	Farchau	D	x	x	10°40′	53°39′	55	8.33	15.00	678	319	25.5
30	Belzig	D	x		12°25′	52°03′	140	8.57	15.56	558	282	31.7
35	Hinterstoder	A	x	x	14°06′	47°43′	1250	2.35	9.20	1495	779	7.6
36	Eisenerz	A	x	x	14°51′	47°32′	1100	2.94	9.96	1168	648	10.4
39	Jaworze	PL	x	x	19°10′	49°50′	450	6.31	13.88	903	533	18.1
43	Jawornik	PL	x	x	22°49′	49°15′	900	6.34	14.12	762	433	21.5
50	Janov	CZ	x		13°15′	50°34′	800	5.03	11.92	826	415	16.9
53	Masun	SLO	x		14°23′	45°38′	1000	7.53	14.38	1346	577	12.6
55	Javor	SLO	x		14°21′	45°44′	1040	8.07	14.98	1345	586	13.1
62	Aarberg	CH	x		7°15′	47°02′	530	8.82	15.46	892	437	20.0
67	Bilowo	PL	x	x	18°10′	54°20′	250	5.82	13.20	633	336	24.6
Trial sites												
2019	Zbraslav	CZ			14°37′	49°95′	360	8,25	15,62	532	330	33,5
2020	Tále	SK			19°03′	48°63′	850	6,58	14,14	842	441	19,1

T—provenances sampled in the trial Tále, Z—provenances sampled in the trial Zbraslav, *T*mean—mean annual temperature, $T_{5–9}$—mean temperature of the vegetation season, *P*year—annual sum of precipitations, $P_{5–9}$—sum of precipitations of the vegetation season, EQ—Ellenberg's quotient

Table 2 Number of days with maximal daily air temperature within each temperature range counted since May 1 until the sampling date (July 2013/2014 for the stressed and June 2016 for non-stressed treatment)

Temperature (°C)	Stressed		Non-stressed	
	Colder plot Tále	Warmer plot Zbraslav	Colder plot Tále	Warmer plot Zbraslav
≥ 32.5	0	2	0	0
30.0–32.5	1	3	0	0
27.5–30.0	5	7	2	1
25.0–27.5	9	7	2	6
< 25.0	56	49	54	39

precisely, air temperatures were repeatedly measured using a Hg thermometer. The average maximum air temperature inside the flask was 29.5 °C and 49.5 °C for water temperatures of 30 °C and 51 °C, respectively; we refer to these temperatures as air temperatures henceforth. At each temperature, a new leaf from the same branch was removed, and two measurements per leaf were performed; nearly 5000 measurements were ultimately analysed. A plant efficiency analyser (Handy PEA, Hansatech, Kings Lynn, UK) was used to measure chlorophyll fluorescence. After a 30-min dark adaptation period, the samples were irradiated by a one-second-long saturation pulse of 3500 µmol m^{-2} s^{-1}. The following parameters were subsequently determined: the basal fluorescence (F_0) measured 50 µs after illumination; the maximum fluorescence (F_m); and F_v/F_m, which was calculated as the ratio of the variable fluorescence ($F_v = F_m - F_0$) to the maximum fluorescence emission (F_m). In addition, the photosynthetic performance index (PI) was evaluated at a temperature of 29.5 °C, which is generally considered non-stressing (Kalaji et al. 2017). The PI was calculated as follows: $\mathrm{PI} = (\mathrm{RC/ABS}) \times [\varphi P_0/(1 - \varphi P_0)] \times [\psi E_0/(1 - \psi E_0)]$, where RC/ABS is the density of PSII reaction centres, φP_0 is the maximum quantum yield of PSII photochemistry and ψE_0 is the efficiency with which a PSII-trapped electron is transferred from Q_A^- to plastoquinone (Strasser et al. 2000; Stirbet et al. 2018).

Data analysis

The thermal sensitivity of PSII was assessed by three parameters:

1. T_{15}, the temperature at which F_v/F_m declines 15% from the maximum value (Froux et al. 2004). The F_v/F_m values were plotted against temperature and fitted to a third-order polynomial from which the T_{15} values were derived (cf. Snider et al. 2013). T_{15} was used as a proxy of the capacity of PSII to resist to heat stress.
2. R, the ratio of the minimum F_v/F_m value (in all observation years, the value attained at 46.7 °C was used) to the initial value (29.5 °C). R was considered a measure of the severity of heat stress; a high R means a relatively low level of stress.
3. T_c, the critical temperature at which the basal fluorescence F_0 started to increase (Lazár and Ilík 1997; Bigras 2000), indicating a threshold for the sharp impairment of PSII. As this increase generally happened between 41.2 and 44.0 °C, T_c was determined as the intersection of linear regression lines, to which the values 29.5–41.2 °C and 44.0–46.7 °C, respectively, were fitted.

Statistical analyses of chlorophyll fluorescence and PSII thermostability data were performed via SAS 9.1.3 (SAS/STAT Software, SAS Institute 2009). Differences among provenances were tested using mixed-model analyses of variance (ANOVA, the MIXED procedure, and type III sums of squares were used throughout the study because of unbalanced designs) under restricted maximum likelihood following the model:

$$\begin{aligned} y_{ijklm} = {} & \mathrm{trial}_i + \mathrm{treatment}_j + \mathrm{prov}_k + \mathrm{trial}_i \times \mathrm{treatment}_j \\ & + \mathrm{trial}_i \times \mathrm{prov}_k + \mathrm{treatment}_j \times \mathrm{prov}_k \\ & + \mathrm{block}_l\left(\mathrm{trial}_i \times \mathrm{prov}_k\right) + \varepsilon_{ijklm}, \end{aligned}$$

where y_{ijklm} is the observed phenotypic value (e.g. F_0 or T_c); trial_i is the effect of the ith trial; $\mathrm{treatment}_j$ is the effect of the jth treatment (year with natural heat stress exposure versus year without natural heat stress exposure); prov_k is the effect of the kth provenance; $\mathrm{trial}_\mathrm{i} \times \mathrm{treatment}_j$, $\mathrm{trial}_i \times \mathrm{prov}_k$, and $\mathrm{treatment}_j \times \mathrm{prov}_k$ are the trial-by-treatment, trial-by-provenance and treatment-by-provenance interactions, respectively; block_k $(\mathrm{trial}_i{\times}\mathrm{prov}_j)$ is the effect of the kth block; and ε_{ijklm} is the experimental error. Because we were interested in particular sites and sets of particular provenances, all effects except the random effects of the blocks were considered fixed. Only the provenances planted on both sites were considered in the ANOVA. Because interactions were generally significant, separate ANOVAs were performed for each treatment, and pairwise contrasts between trial sites were calculated within each treatment, while least-square estimates of the means were derived for each provenance. We subsequently looked for geographical and ecological patterns in the performance of provenances. The provenance means were displayed geographically using QGIS v. 2.8.1 software (http://www.qgis.org). Furthermore, the means were regressed against altitude and climatic variables of the sites of origin (linear and quadratic regressions); the REG procedure (SAS Institute 2009) was used.

To assess the geographical trends of photosynthetic performance and PSII thermostability, physiological parameters (provenance averages) were correlated with the spatial distance of the site of origin from the trial site and from the supposed glacial refugia. Geographical coordinates (longitude, latitude) were converted into rectangular ones in a Lambert conformal conic projection using CoordTrans v.2.3 software (Franson Technology AB, Stockholm, Sweden; http://franson.com/coordtrans), and Euclidean distances between sites were calculated. Because the exact position of the refugial population is unknown, the position of the Slovenian population Javor was used as a proxy. This analysis was carried out only for the Tále site, which had a larger sample size than did the other site.

Results

Variation in chlorophyll a fluorescence

Almost all the chlorophyll *a* fluorescence parameters differed significantly ($P < 0.05$) or marginally significantly ($P < 0.10$) between the treatments and plots (Table 3) at a non-stressing temperature (29.5 °C). The interannual shifts in PSII performance were not completely consistent, but the correlations between years were generally significant at both trial plots. The performance of PSII (as measured by the *PI*) was better after natural heat stress exposure than at the beginning of vegetation season (Table 3). In the warmer trial plots at Zbraslav, the performance of PSII was generally better than that in the plots at Tále in both years of observation, although the differences were quite small and even not significant for some parameters. The trial-by-treatment interactions were significant for F_0 and the PI (Table 3), indicating that the response of photosynthetic performance to natural heat stress exposure differed between the sites. On the other hand, the responses of the provenances to the treatments were quite consistent; the treatment-by-provenance interactive effects were mostly not significant.

The overall PSII performance of the provenances did not show any range-wide trends, but a certain geographical pattern was recognizable and consistent among the different parameters, at least in the trial plots at Tále, where the sample size in terms of the number of provenances was sufficient for a quantitative analysis. In general, populations close to the Slovenian refugia (Slovenia, the Western Carpathians, the Sudetes) showed better performance, which decreased towards the western and northern range margins (Fig. Suppl. 2a, b); however, this effect was clearly more pronounced in the year with heat stress exposure. To a certain degree, the

Table 3 Analysis of variance of chlorophyll *a* fluorescence parameters at 29.5 °C (degrees of freedom and significance of *F* tests and *Z* tests), including trial plot means and standard deviations for both treatments (before and after natural heat stress exposure), and between-treatment correlations

Source of variation	*DF*	F_0		F_v/F_m		PI	
Fixed effects		*F*[a]	*P*[b]	*F*	*P*	*F*	*P*
Trial[c]	1	3.52	0.1572	13.63	0.0345	7.48	0.0717
Treatment	1	3.06	0.0810	2.91	0.0890	110.55	<0.0001
Provenance	9	3.93	<0.0001	7.51	<0.0001	7.50	<0.0001
Trial*provenance	9	2.77	0.0037	2.94	0.0022	3.70	0.0002
Trial*treatment	1	30.46	<0.0001	2.13	0.1449	26.88	<0.0001
Treatment*provenance	9	1.37	0.2005	0.85	0.5726	1.44	0.1683
Trial*treatment*provenance	9	2.53	0.0079	1.65	0.0985	1.67	0.0942
Error	399						
Random effect		*Z*[d]	*P*	*Z*	*P*	*Z*	*P*
Block (trial*prov)	20	0.94	0.1744	0.99	0.1604	0.72	0.2532

Trial plot	F_0		F_v/F_m		PI	
	Tále	Zbraslav	Tále	Zbraslav	Tále	Zbraslav
Non-stressed						
Mean	0.422	0.453	0.781	0.797	18.48	18.36
SD	0.031	0.036	0.027	0.013	7.01	5.27
P[e]	<0.0001		<0.0001		0.8481	
Stressed						
Mean	0.431	0.429	0.783	0.803	21.97	27.47
SD	0.040	0.046	0.027	0.016	6.87	7.49
P[b]	0.2648		<0.0001		<0.0001	
Correlation[f]						
r	0.586	0.293	0.552	0.775	0.643	0.551
P	0.0135	0.4122	0.0217	0.0084	0.0054	0.0988

[a] *F* test statistics

[b] Significance

[c] *DF* (denominator) = 3

[d] Wald *Z* score

[e] Difference between trial sites, *F* test

[f] Pearson's correlation coefficients between provenance averages of physiological parameters between stressed and non-stressed trees

same trend occurred in relation to the distance of the site of origin from the site of plantation (Table 4). The chlorophyll *a* fluorescence parameters also showed significant associations with climate of origin: the PSII performance was generally higher in provenances originating from colder and wetter climates than in provenances originating from warmer and drier ones.

Thermostability of photosystem II

The mean response curves of the maximum quantum yield of PSII photochemistry (F_v/F_m) to temperature are shown in Fig. 1. Naturally, there was variation among trees and provenances (Fig. Suppl. 2c), but the figure shows the typical behaviour of chlorophyll fluorescence in response to simulated heat stress at both trial sites and for both treatments. At Zbraslav, the values usually remained quite stable up to 42 °C, but afterwards, the decrease was slow compared to that at Tále for both treatments. At Tále, F_v/F_m remained quite stable until 38 °C, after which it slightly decreased; past 44 °C, it decreased abruptly. The decrease was much more pronounced for previously stressed trees. This difference in the shape of the response curve of course affected not only the thermal limit of PSII resistance T_{15} but also the severity of thermal stress *R*.

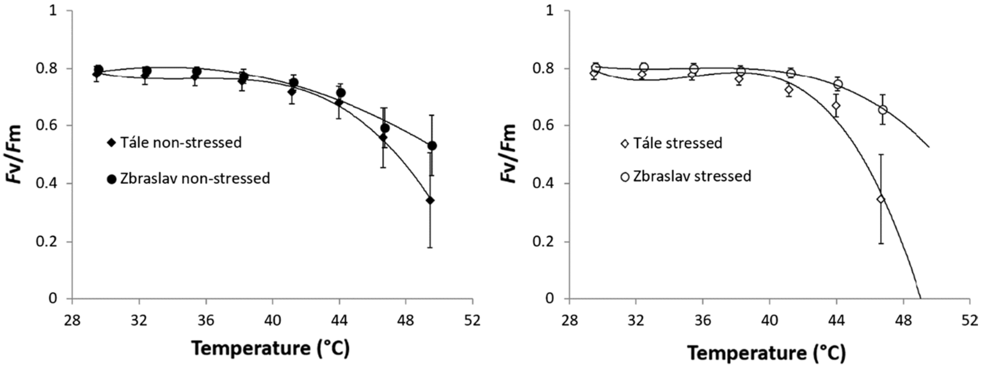
The severity of heat stress *R* was significantly affected by all three factors (Table 5). The response of PSII to weather conditions as measured by *R* clearly differed

Table 4 Correlations of PSII thermostability and/or chlorophyll *a* fluorescence parameters vs. aerial distances from the sites of origin to the Slovenian refugium and/or Tále trial plot

		T_{15}	R	T_c	F_0	F_v/F_m	PI
Non-stressed							
Distance from refugium[a]	r	− 0.2340	− 0.3998	− 0.3444	0.3497	− 0.4957	− 0.5275
	P	0.3660	0.1118	0.1758	0.1688	0.0430	0.0295
Distance from trial plot	r	− 0.1433	− 0.4231	− 0.3952	0.0187	− 0.4227	− 0.4419
	P	0.5833	0.0906	0.1433	0.9431	0.0910	0.0757
Stressed							
Distance from refugium[a]	r	− 0.4148	− 0.2382	− 0.0140	0.1653	− 0.6957	− 0.7581
	P	0.0978	0.3572	0.9576	0.5261	0.0019	0.0004
Distance from trial plot	r	− 0.4031	− 0.2593	− 0.1058	0.2039	− 0.5512	− 0.7203
	P	0.1086	0.3148	0.6862	0.4324	0.0218	0.0011

[a] Distance from the Slovenian population Javor

Fig. 1 Average response curves of the maximum quantum yield of PSII photochemistry (F_v/F_m) to temperature at different trial sites in the terms before and after a natural heat stress event



between the observation years: after exposure to heat (in July 2013/2014), R was substantially higher and less variable at Zbraslav than at Tále, whereas without exposure (in June 2016), the difference between the sites was negligible and not significant. A similar result (albeit less pronounced) was observed for T_{15}. In the year of heat stress, the average T_{15} was almost 3 °C higher at Zbraslav compared to Tále, whereas without exposure to stress, the difference between sites was not significant.

The provenance means were displayed on a map (Fig. 2a, b) and regressed against the climate characteristics of the sites of origin separately by site and year of observation (see also Suppl. 1b). In the years with heat stress, the distribution of T_{15} showed geographical patterns for both trials, although they were not completely clear. At Tále, the highest thermotolerance was observed in central European populations, whereas low T_{15} values were found in marginal populations, especially at the north-western periphery but also at the eastern limit. One clear outlier at both Tále and Zbraslav was the non-indigenous Scottish population Westfield. In the case of R, similar geographical patterns were observed; they were less pronounced but still discernible. Again, at Tále the most severe decrease in F_v/F_m was observed in the populations at the northern and eastern distribution limits, whereas at Zbraslav, the values exhibited a west–east trend. There was, nevertheless, a striking difference in the range of provenance averages between the plots, which was much smaller at Zbraslav (0.08) compared to Tále (0.30). On the other hand, the geographical pattern of thermotolerance indicators in the year without heat stress was chaotic; no clear spatial patterns or trends could be distinguished for either trial plot (Fig. 2a, b).

In contrast to the overall photosynthetic performance assessed by chlorophyll fluorescence, the thermostability parameters did not show significant correlations with the distance from either the refugia or trial plots (Table 4).

Because several trial-by-provenance and trial-by-treatment-by-provenance interactions were significant (i.e. the provenances responded differently to the environments at the trial sites in different years), we examined the relationships between PSII thermostability parameters and the climatic characteristics of the sites of origin separately by trial site and year. Although most regression models were non-significant or marginally significant ($P < 0.10$), there was a clear difference between the behaviour of provenances in different trials after exposure to natural heat stress (Table 6). At Tále, the thermotolerance decreased linearly with both increasing temperature and decreasing precipitation at the site of origin of the provenances, while at Zbraslav, the response was consistently nonlinear. In the year without heat stress, consistent

Table 5 Analysis of variance (degrees of freedom and significance of *F* tests and *Z* tests) of PSII thermostability parameters, including trial plot means and standard deviations for both treatments (before and after natural heat stress exposure), and between-treatment correlations

Source of variation	*DF*	T_{15}		*R*		T_c	
Fixed effects		*F*[a]	*P*[b]	*F*	*P*	*F*	*P*
Trial[c]	1	88.53	0.0025	15.10	0.0302	7.69	0.0694
Treatment	1	4.01	0.0467	55.26	< 0.0001	0.80	0.3708
Provenance	9	0.83	0.5927	1.94	0.0480	2.64	0.0067
Trial*provenance	9	1.42	0.1830	1.55	0.1321	2.00	0.0410
Trial*treatment	1	52.61	< 0.0001	146.05	< 0.0001	0.03	0.8521
Treatment*provenance	9	1.12	0.3520	2.92	0.0029	0.84	0.5783
Trial*treatment *provenance	9	1.98	0.0439	2.04	0.0372	0.98	0.4552
Error	199						
Random effect		*Z*[d]	*P*	*Z*	*P*	*Z*	*P*
Block (Trial*Prov)	20	1.72	0.0338	0.71	0.2404	0.62	0.2684

Trial plot	T_{15}		*R*		T_c	
	Tále	Zbraslav	Tále	Zbraslav	Tále	Zbraslav
Non-stressed						
Mean	44.24	44.68	0.7232	0.7464	43.16	42.14
SD	1.87	1.43	0.1268	0.0782	1.94	2.51
P[e]	0.2082		0.2983		0.0049	
Stressed						
Mean	43.33	46.22	0.4341	0.8168	43.42	42.24
SD	0.66	1.14	0.1849	0.0607	0.48	2.22
P[b]	< 0.0001		< 0.0001		< 0.0001	
Correlation[f]						
r	− 0.035	− 0.448	− 0.024	− 0.559	0.263	0.476
P	0.8920	0.1945	0.9261	0.0925	0.3080	0.1639

[a] *F* test statistics

[b] Significance

[c] *DF* (denominator) = 3

[d] Wald *Z* score

[e] Difference between trial sites, *F* test

[f] Pearson's correlation coefficients between provenance averages of physiological parameters between stressed and non-stressed trees

responses were observed only at Tále: *R* again decreased with increasing continentality (i.e. increasing temperatures and decreasing precipitations) at the site of origin (Table 6).

Discussion

Effects of temperature on photochemistry

As we were interested in the stability of PSII in response to high temperature, the range of tested temperatures was quite narrow such that we were able to capture precise changes in the response. However, the response curves were generally flat and sharply decreased on their right side: the photosynthetic performance measured by all chlorophyll fluorescence parameters was generally constant between 29.5 and 41 °C, and sharp changes occurred mostly above 44 °C. Such a response pattern is typical for chlorophyll fluorescence (Brestic and Zivcak 2013), but there are significant differences in response to heat among plant species. T_c typically ranges from 32 to 48 °C for temperate-origin species (Weng and Lai 2005). The threshold for heavy damage to PSII of beech, and in broadleaf trees in general, is higher than that of most annuals (Dreyer et al. 2001; Weng and Lai 2005). In our study, the mean T_c was approximately 43 °C. However, it should be taken into account that the threshold was measured after short-term heat stress, while a prolonged effect of high temperature causes an increased reduction

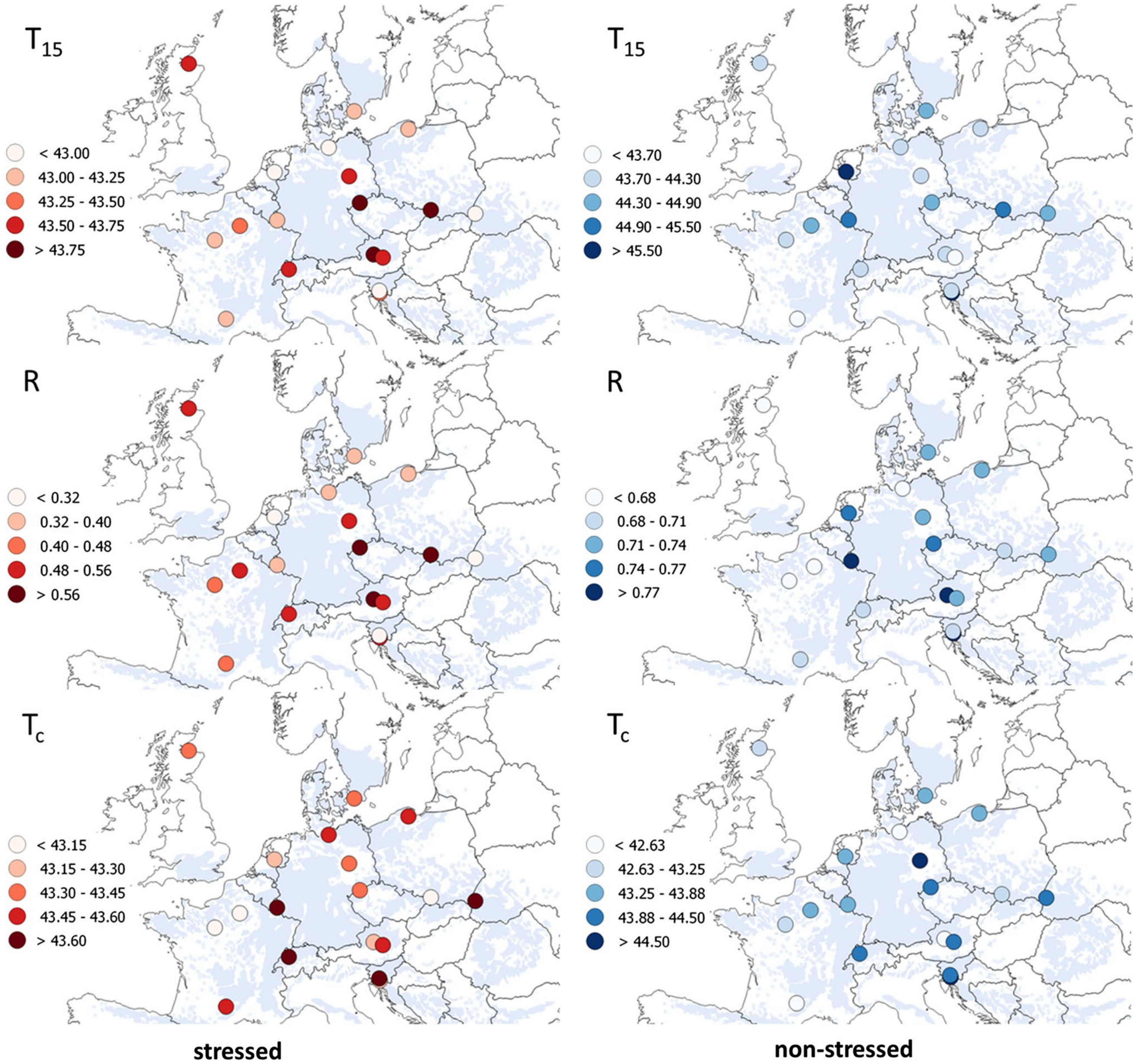


Fig. 2 **a** Geographical distribution of T_{15} (up), R (middle) and T_c (down) at the Tále trial site under (left) and without (right) natural heat stress. The means per provenance are displayed by different colours at different intervals. There are two provenances from Croatia and one is largely overlapped. **b** Geographical distribution of T_{15} (up), R (middle) and T_c (down) at the Zbraslav trial site under (left) and without (right) natural heat stress. The means per provenance are displayed by different colours at different intervals

(Georgieva et al. 2000). Dreyer *et al.* (2001) estimated a T_c of 46.3 °C for *Fagus sylvatica* during gradual (short-term) increases in temperature but noticed a decrease in F_v/F_m at temperatures as low as those between 32 and 38 °C if the trees were exposed to high temperatures for 12 h. Moreover, high temperatures may influence young unshaded trees even more significantly if they are unshaded by mature stands, and additional light may cause photoinhibition and oxidative stress and could downregulate PSII photochemistry. This phenomenon is an especially important threat to plantations of beech seedlings in open fields or in large forest gaps. Depending on the stress intensity, PSII recovery may prevail after only 3 days (Ghouil et al. 2003). Heat periods can significantly hinder the culmination of seasonal diameter increase and reduce the competitive strength of beech.

Local adaptation or demography?

Studying the same set of beech provenances, Gömöry et al. (2015) showed that differentiation of chlorophyll

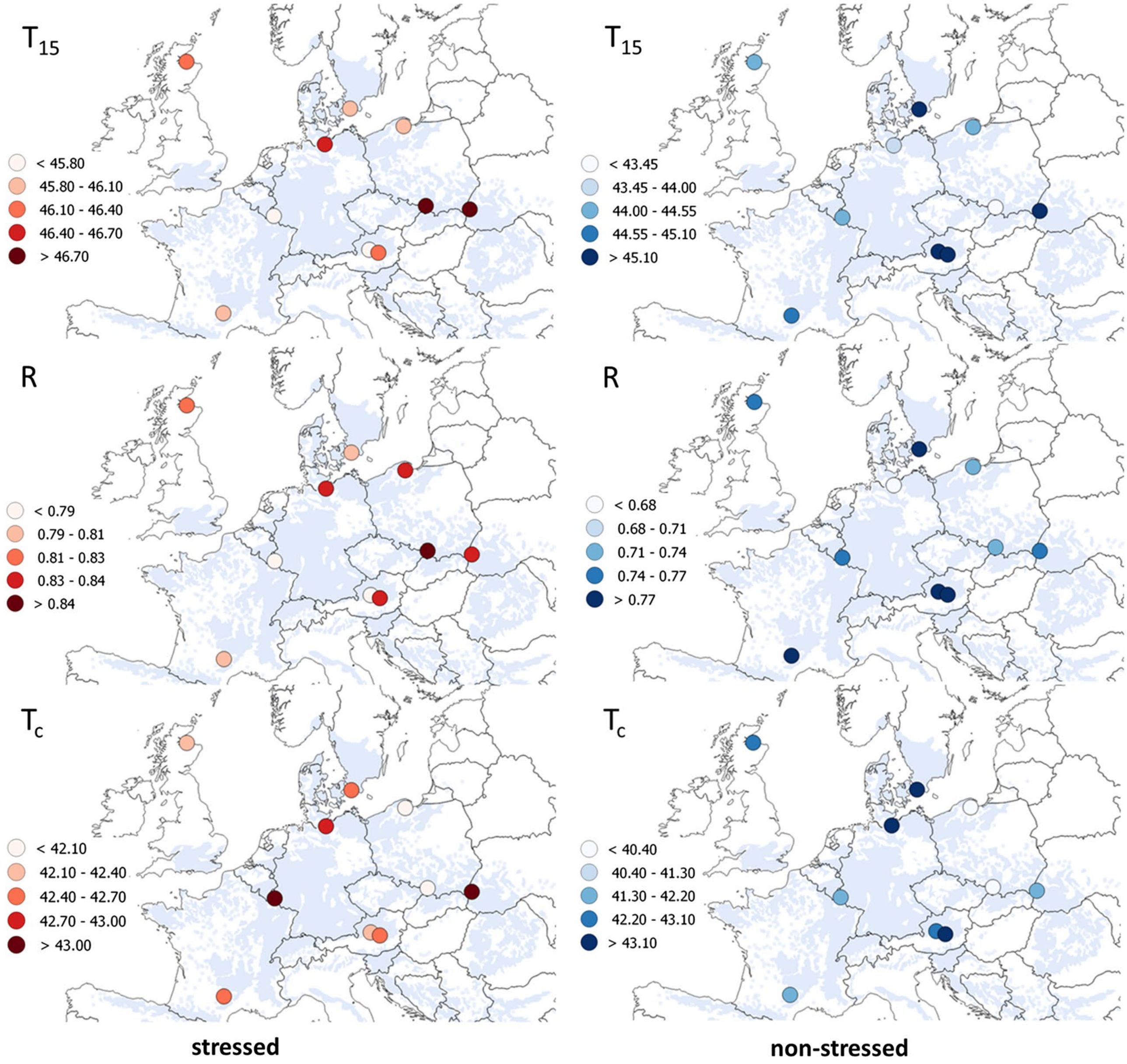


Fig. 2 (continued)

fluorescence traits was generally low and comparable to the differentiation of neutral markers, i.e. loci not underlying natural selection. This phenomenon would suggest a lack of local adaptation of physiological traits, which could be due to either the absence of selection pressure or stabilizing selection. For quantitative traits showing low levels of differentiation, these two cases are difficult to distinguish unless large sample sizes are used because differentiation at neutral loci is typically very low in anemophilous trees with large continuous ranges (cf. Comps et al. 2001; Buiteveld et al. 2007; Gömöry et al. 2007). Low phenotypic differentiation found by listed authors is in contrast with significant inter-provenance differences and/or plot-by-provenance interactions that we observed in the current study both for chlorophyll fluorescence and thermostability parameters.

In response to stress imposed by high temperatures under field conditions, most parameters exhibit quite clear geographical patterns, with high (better) values in Central Europe decreasing in all directions towards the range margins. This is true mainly for the performance of PSII and is less true for thermostability. Moreover, in the present study, the trends were inconsistent between years with and without natural heat stress exposure. The existence of inter-population or inter-genotype physiological variation, which is sometimes attributable to geographical origin, has been observed in beech and other plant species (Rose et al.

Table 6 Linear and quadratic regressions of T_{15} and R against climate characteristics at the sites of origin of beech populations (significant and marginally significant models are shown)

Variable[a]	Linear model			Quadratic model		
	Slope	P	R^2	Ext[b]	P	R^2
Tále, stressed—T_{15}						
T_{mean}	−0.0850	0.0461	0.2262			
$T_{5–9}$	−0.1030	0.0345	0.2501			
BIO5				223.2	0.0923	0.2721
BIO10				161.9	0.0551	0.3206
BIO18	0.0018	0.0678	0.1935			
Tále, non-stressed—T_{15}						
$T_{5–9}$				12.94	0.0841	0.2812
BIO5				208.4	0.0853	0.2798
Zbraslav, stressed—T_{15}						
$P_{5–9}$				508.6	0.0569	0.5591
BIO4				5579	0.0523	0.5696
BIO7				236.5	0.0706	0.5311
BIO8				67.7	0.0273	0.6426
BIO18				338.0	0.0148	0.6997
Zbraslav, non-stressed—T_{15}						
	ns			ns		
Tále, stressed—R						
	ns			ns		
Tále, non-stressed—R						
T_{mean}	−0.00900	0.0455	0.2271			
P_{mean}	0.000077	0.0370	0.2444			
$P_{5–9}$	0.000137	0.0526	0.2150			
BIO10	−0.00104	0.0880	0.1711			
BIO18	0.000196	0.0579	0.2068			
EQ	−0.00365	0.0214	0.2891			
Zbraslav, stressed—R						
BIO4				5642	0.0931	0.4924
BIO8	0.000433	0.0148	0.5447			
Zbraslav, non-stressed—R						
	ns			ns		

[a] Designation of variables as in Table 1

[b] Value at which the regression function attains maximum or minimum, ns—no significant model

2009; Brestic et al. 2012; Aranda et al. 2015) and suggests a hereditary basis (genetic or epigenetic) of the traits in question. However, their underlying mechanisms are difficult to identify without ambiguity. In genetic data such as single nucleotide polymorphisms, a plenty of methods are available for distinguishing between the imprints of divergent selection and demographic processes such as migration, gene flow or reduction in population sizes (Li et al. 2012; Wu et al. 2014; Fijarczyk and Babik 2015). On the other hand, explicit testing of the adaptation vs. demography hypothesis in phenotypic clines is more difficult.

We observed climate-related clines in PSII thermostability in both trial plots, although the shape of the response function differed between the trials. Clinal or cline-like trends were also observed in previous studies on the variation in photosynthetic performance of beech (Robson et al. 2012; Stojnić et al. 2012). On the other hand, an abrupt change in net photosynthesis between north-western and south-eastern beech provenances, as reported by Paludan-Müller et al. (1999), underlines the need for considering historical and demographic factors in the interpretation of climatic differences and trends. In this case, the difference is clearly linked with the origin from different refugia. In our study, climatic gradients partly overlap with the routes of the Holocene expansion of beech (cf. Magri et al. 2006). Migration in beech, which is a zoochorous species, is associated with a reduction in allelic richness at the leading edge due to recurrent bottlenecks (Comps et al. 2001), which may potentially limit the adaptation potential of marginal populations and, consequently, reduce their physiological performance.

The PSII performance of beech provenances at the Tále site being negatively correlated with the distance from the site of plantation can be taken as a sign of local adaptation. As postulated by Kawecki and Ebert (2004; the ‘local vs. foreign’ criterion), compared with demes originating from elsewhere, a local deme is expected to be superior in terms of fitness. However, we found that correlation coefficients for the distance from the refugia (the approximate distance of the exact location of the Slovenian/Istrian refugium is unknown) are more or less the same. The fact that the peak T_{15} and R values were observed not in Slovenia but were farther to the north and close to the plantation site cannot be taken as an argument favouring adaptation as the background mechanism.

In 2016, when sampling was accomplished prior to the occurrence of extreme temperatures, the performance of PSII as measured by the PI was surprisingly better than in the years with heat exposure (Table 3). This finding could be due to the seasonal dynamics of the relative proportions of pigments. Drought was probably a negligible factor in this response, as sampling was performed in June and during the first third of July when soil is still usually wet. The geographical patterns of the thermostability parameters are chaotic in the year without heat stress, and the PSII performance decreased towards the range periphery. These results indicate that the mechanisms underlying PSII performance and PSII thermostability under different conditions are not identical (Fig. 2a, b). These findings are consistent with those of Carsjens et al. (2014), who studied proteins involved in abscisic acid-related drought signalling in beech and demonstrated that the expression levels differ among the controlling genes, which were constitutively up/downregulated depending on the climate of origin in some cases and dynamically reflected the actual stress in the other cases. Whatever the physiological and biochemical background of thermostability, it seems to be induced by heat stress experienced during the ongoing growing season. In contrast to PSII performance, the memory of such stress does not persist until the following year; this phenomenon is also documented by weak and non-significant between-year correlations.

No spatial trend was observed for the critical temperature that causes abrupt changes in F_0 (T_c) indicating impairment of PSII. This fact may be the result of a purely technical phenomenon: the response to the rise in temperature did not always exhibit an abrupt change bur rather increased quite continuously, although the increase slightly accelerated at relatively high temperatures (cf. Bigras 2000). An exact determination of T_c would require shortening the temperature intervals around the critical temperature. Although differences in T_c among the provenances were significant, the provenance averages seemed to be affected by a large experimental error, leading to chaotic geographical trends. The absence of trends confirms the observations of Froux et al. (2004), in which changes in F_v/F_m are caused by a decrease in maximum fluorescence rather than by an increase in basal fluorescence.

In any case, the population effect on PSII properties was always negligible compared to the effects of plantation site and exposure to heat stress. In an observational experiment, explicit testing of the mechanisms underlying such outcomes is difficult; however, it is probable that a combined effect of regular exposure of trees growing at Zbraslav to heat, light, and drought stress increased their tolerance, and they did not respond to high daily temperatures that occurred prior to sampling. At Tále, where extreme events occur less often, similar conditions could lead to damage to PSII in the field, incomplete regeneration during the night, and decreased average performance of samples when measured under standard non-stressing conditions. Differences between sites with respect to the response of PSII thermostability to prior heat stress were even more clear. The thermostability parameters derived from the maximum quantum yield showed a similar response pattern. In the absence of temperature stress (in June), however, the values did not differ between the sites, whereas after exposure to heat (in July), the photosynthetic performance of beech was better at Zbraslav, which is climatically warmer and drier than Tále is. The response curve of maximum quantum yield to increasing temperature was rather flat at Zbraslav, which means that the severity of the stress was generally substantially smaller and that PSII retained functionality at much higher temperatures at that site than at Tále. This finding is indicative of phenotypic plasticity, i.e. the ability of genotypes to produce different phenotypes under different environments, which is known to be a typical feature of trees because of their longevity (Bussotti et al. 2015; Schuldt et al. 2016; Stojnić et al. 2015). It is important to note that, because the survival rates of the tested provenances are relatively high (more than 70%) and comparable at both sites (Alía et al. 2001), the difference between the sites does not result from divergent selection for PSII thermostability at the juvenile stage; rather, acclimation triggered by differential exposure to heat events in the long term is a more plausible explanation.

Conclusions

Provenance trials serve as an important source of information about tree population responses to climate (Mátyás 1994). Although the space-for-time-substitution approach has limitations, it is the best available option for the prediction of the behaviour of tree populations under future, warmer climates. Provenance research has traditionally focused on variation in economically important traits such as growth or tree architecture. Our study represents a new direction in this line of research and is step towards a multidisciplinary approach, a deeper understanding of forest ecosystems and a possible solution of future issues associated with ongoing climate change. This study aims to characterize the within-species variation in physiological traits and identify the underlying evolutionary and ecological mechanisms. The experimental setup, which was based on measurements under standardized conditions performed on material collected from identical sets of populations planted at different sites, allowed separating the hereditary (population) effects from those of the growth environment. Our results suggest that, despite a certain level of hereditary variation in performance and thermostability of PSII, which is associated with the site of origin, acclimation driven by the climate of the plantation site and the weather during the present growing season play a more important role. In the context of climate change, our findings indicate that beech seems to be capable of maintaining a functioning photochemistry under recurrent heat stress and that its ability to adjust is not substantially limited by hereditary constraints. Another challenge for the future is to investigate the combination of abiotic factors and determine the extent of their synergistic or possible antagonistic effects.

Acknowledgements The provenance experiment has been established through the realization of the project European Network for the Evaluation of the Genetic Resources of Beech for Appropriate Use in Sustainable Forestry Management (AIR3-CT94-2091) under the coordination of H.-J. Muhs and G. von Wühlisch. The experimental plots Tále and Zbraslav were established by L. Paule and V. Hynek, respectively. The study was supported by research grants of the Slovak Research and Development Agency APVV-0135-12, by the project of the Ministry of Agriculture of the Czech Republic—institutional support MZE-RO0118 and by the Research Agency of the MESRS of the SR, Project No. ITMS 26220220066 (20%). International cooperation in the study of physiological variability of beech provenances was established within the COST action FP1202 Strengthening conservation: a key issue for adaptation of marginal/peripheral populations of forest trees to climate change in Europe (MaP-FGR).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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