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Photosynthetic performance of silver fir (*Abies alba*) of different origins under suboptimal growing conditions

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Abstract. Understanding of the intraspecific variability in the physiological stress response of trees may enable to mitigate the impact of climate change on forest ecosystems in the future. We studied the photosynthetic performance of five silver fir (*Abies alba* Mill.) provenances originating from climatically distinct localities. The study was performed in the trial plot of the silver fir provenance experiment IUFRO 2005 on two dates: in the early summer and in the late summer. Heat waves and a decrease in water availability occurred between the two measurement dates, allowing us to study the response of the provenances to suboptimal growing conditions. The provenances were evaluated at the level of PSII photochemistry and CO_2 assimilation by measuring photosynthesis-related pigment content, chlorophyll *a* fluorescence, and gas exchange parameters. Significant climatic clines were confirmed: the photosynthetic performance before and after the stress period increased with the increasing altitude and precipitation at the site of origin. In contrast, photosynthetic performance declined with the increasing temperature and Ellenberg's quotient of the origin site. We concluded that provenances originating from high altitudes, corresponding well with more humid and colder conditions in Central Europe, showed the greatest photosynthetic performance and were less responsive to moderate heat and drought. This documents inter-population variation in physiological traits, which needs to be considered in setting rules and recommendations for the transfer of forest reproductive materials.

Additional keywords: assimilatory pigments, assimilation rate, common garden, fast kinetics of chlorophyll *a* fluorescence, rapid light curves.

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Introduction

The response of tree species to ongoing climate changes, including more frequent and intense heat and drought, is difficult to predict. The utilisation of the available adaptive divergences within species and the introduction of new, well adapted provenances suitable for future environmental conditions are, therefore, considered particularly important measures for maintaining the stability and productivity of forest ecosystems in the future (Matyas 1994; König 2005; Kremer *et al.* 2012). However, most provenance studies have been restricted to the most common species and have been

performed under controlled or semi-controlled conditions at the juvenile stage (Robakowski *et al.* 2002; Pšidová *et al.* 2015; Bolte *et al.* 2016; Matías *et al.* 2016; Jamnická *et al.* 2019), which cannot fully represent real environmental conditions and cannot be confirmed by later practical experience (Kerr *et al.* 2015; Voltas *et al.* 2018). Research dealing with processes underlying production and survival in field conditions is quite scarce (e.g. Wortemann *et al.* 2011; Hajek *et al.* 2016; Konôpková *et al.* 2018; Kurjak *et al.* 2019) and it is mostly restricted to fitness proxies such as height, diameter at breast height, basal diameter, mortality and phenology of trees (Robson *et al.* 2018). Therefore, the study of the physiological processes in mature trees along climatic and geographic gradients could provide useful insights into genetic adaptive variability, allowing us to model and predict tree responses to rapidly changing environment (König 2005; Kremer *et al.* 2012). Moreover, to the best of our knowledge, very little detailed data about physiology are available for populations of silver fir.

Silver fir (Abies alba Mill.) is one of the most productive and ecologically valuable native conifers in European mountain forests (Dobrowolska et al. 2017; Vitasse et al. 2019). In forestry, special attention has been paid to firs due to their widely described dieback and decline between the 1970s and 1980s. However, pollution control and changes in forest management during recent decades have facilitated the recovery of fir stands throughout Europe (Bošela et al. 2014; Büntgen et al. 2014) and currently, silver fir is of interest in many studies (Bouriaud and Popa 2009; Vitali et al. 2017; Vitasse et al. 2019) as a potential replacement for spruce. Silver fir has a broad range of desirable properties that make it better-suited for forests across Europe than spruce: it is a native tree species that is more resistant and resilient to drought extremes (Bouriaud and Popa 2009; Vitali et al. 2017), and it shows a positive reaction to a slight temperature increase in the late winter and early summer (Castagneri et al. 2014; Bosela et al. 2016).

Although fir has responded well to changes in the environment over the last decades, its resilience and ability to adapt to the predicted climate changes may be severely compromised (Dobrowolska et al. 2017). In Central Europe, isotherms at the same altitude could be shifted up to 300-500 km per 100 years; this shift is far greater than the natural migration ability of most woody species, which generally did not exceed 10-40 km per 100 years during the Holocene expansion (Mátyás 2007). The estimated migration ability of fir is 16-24 km per 100 years (Cheddadi et al. 2014). Therefore, the trees will be probably unable to migrate fast enough to track the projected changes without human assistance. Assisted migration - the artificial planting of appropriate reproductive materials coming from geographically distant populations - has been proposed as a strategy for mitigation of climate change impacts on forest ecosystems.

An appropriate tool for the study of potential sources of reproductive material is provenance research, a common garden experiment including populations of the same species originating from different, rigorously defined geographic areas planted at the same locality. Equal growing conditions eliminate the phenotypic differences between populations caused by a wide range of environmental factors (Sáenz-Romero et al. 2019). Therefore, a provenance trial provides significant information on the level of genetic variation in fitnessrelated traits within and between populations as an outcome of the balance of divergent selection across populations (Kremer et al. 2012; Konôpková et al. 2019). Moreover, provenance trials foresee the effects of climate change based upon the concept that between-provenance genetic variation patterns represent a response to a transfer into a changed environment and may be seen as a simulation of responses to altered climate over time (Huntley et al. 1997).

In this context, we focussed on the study of the photosynthetic responses of 15-year-old silver fir (*Abies alba* Mill.) provenances originating from contrasting environmental conditions but growing in the same experimental plot. The experimental plot was established below the optimal climate conditions for silver fir, with a warmer and less humid climate; however, this location well simulates the conditions that are expected in the silver fir range at the end of the 21st century (Konôpková *et al.* 2018; Vitasse *et al.* 2019). The suboptimal growing conditions in the experimental plot were enhanced in 2015 by a precipitation deficit, and heat waves occurred during the study period as well.

Heat stress can damage PSII at the level of reaction centres, light-harvesting system or oxygen evolving system and affects enzymatic processes (Dreyer et al. 2001; Allakhverdiev et al. 2008; Brestič and Živčák 2013). Drought alters osmotic potential and stomatal conductance, but also mesophyll conductance (von Caemmerer et al. 2014), the content of non-structural carbohydrate (Zlobin et al. 2019) and hydraulic properties (Bréda et al. 2006). Thus, both drought and heat have a direct or indirect adverse effect on primary and secondary photosynthetic processes. In contrast, photosynthesis affects all metabolic and physiological processes and is therefore a reliable measure of overall plant performance (Bussotti and Pollastrini 2017; Kalaji et al. 2018). Hence, we described the photosynthetic performance of individual provenances at the level of PSII photochemistry and gas exchange. The study of photosynthetic processes could help to better understand the intraspecific variation of survivability, development, and production and could be useful in forestry improvement programs (Pšidová et al. 2015; Kučerová et al. 2018; Jamnická et al. 2019).

We hypothesised that the divergence between provenances was driven by different selective pressures imposed by different ecological environments at their origin sites and should also be recognisable after the transfer to a new location. Therefore, the provenances originating from different locations should have different photosynthetic performance and different responses to natural heat and drought events.

The aims of our study were to (i) assess the variability of overall photosynthetic performance in silver fir provenances originating from distinct localities; (ii) determine how different silver fir provenances respond to naturally occurring combined heat and drought stress; and (iii) determine whether the photosynthetic performance of silver fir provenances shows patterns along the geographic and climatic gradients.

Materials and methods

The experimental plot, growth conditions, and plant material

The samplings and *in situ* measurements were performed on a silver fir provenance trial plot in Hertník, eastern Slovakia (49.217°N, 21.271°E; 390 m above sea level). The trial plot was established within the framework of the second international provenance experiment with silver fir organised by IUFRO in 2005 and comprises 17 provenances covering most of the eastern part of the fir distribution range (Tabel 2000). Each provenance was planted in three complete, randomised blocks using 5-year-old plants with an initial number of 35 seedlings per provenance and block.

For the study, we chose five provenances with climatically contrasting origins. To minimise the potential variation caused by non-adaptive processes, only provenances originating from the Apennine (Central European) glacial refugium were included (cf. Liepelt *et al.* 2009). The basic characteristics of the tested provenances are shown in Table 1 and Fig. 1, and the provenance names follow the labelling system of the common database of the provenance experiment. The provenances were examined on two dates in 2015, in early summer (14 July) and in late summer (4 September). Measurements of gas-exchange parameters, chlorophyll *a* fluorescence (by two different methods) and photosynthesis-

related pigment contents were made on each date. All measurements and samplings were conducted on the same set of six trees (two blocks, three individuals per block) for each provenance. All measurements were performed on 1-year-old shoots on the northern side of the crown at breast height.

Meteorological characteristics

Meteorological conditions were continuously monitored in an open field in the middle of the trial plot during the whole growing season of 2015 (April 2015–September 2015). The conditions, including air temperature (°C), relative humidity (%), global incoming solar radiation (W m⁻²) were recorded

Table 1. List of the tested silver fir provenances in the Hertník trial plot and the basic geographic and climatic characteristics of their sites of origin

Abbreviations: PV, provenance; Long, longitude (°); Lat, latitude (°); Alt, altitude (m above sea level); T_{MEAN} , mean annual temperature (°C); T_{59} , mean temperature during the growing season (°C); P_{YEAR} annual precipitation (mm); P_{59} , precipitation of the growing season (mm)

PV	Country	Name	Long	Lat	Lat Alt		T ₅₉	$P_{\rm YEAR}$	P ₅₉
			Ti	rial plot					
TP_H	Slovakia	Hertník	49.217	21.271	390	7.2	15	737	424
			Tested	provenances	1				
PL41	Poland	Kadlubiska	50.300	22.167	250	7.6	15.9	591	354
SK01	Slovakia	Staré Hory	48.750	19.750	500	6.6	14.2	781	447
PL21	Poland	Berest-1	49.550	20.950	690	6.2	13.9	836	486
SK02	Slovakia	Bardejov	49.417	21.250	900	5.6	13.2	849	482
AT	Austria	Koetschach Valey	47.100	13.183	1300	1.8	8.3	1327	692



Fig. 1. Locations of the origins of the tested provenances (black circles) and the Hertník trial plot (star). The grey area represents the natural distribution range of silver fir (adapted from EUFORGEN 2015; www.euforgen.org).

by the Minikin THR (EMS Brno) and rainfall (mm) by the tipping bucket rain-gauge MetOne 370R. Meteorological variables were measured every 2 min and saved in 20-min intervals.

The measurements of soil water potential (Ψ soil, MPa) were continuously recorded in 12 micro-plots at 15, 30 and 50 cm depth using gypsum blocks (Delmhorst Inc.) and MicroLog SP3 datalogger (EMS Brno) up to -1.5 MPa, which is the device limit: 10 micro-plots represented the area of tested provenances and two micro-plots were placed in an open field near the meteorological station. Overall, 36 gypsum blocks were used, 12 for each soil depth. We used the mean values of all the blocks representing the whole site for the analyses to avoid mosaic heterogeneity between and inside the micro-plots.

Photosynthesis-related pigment contents

Sampling was conducted in five repetitions for each individual. The concentration of photosynthesis-related pigments was determined according to Lichtenthaler (1987) using spectrophotometer Cintra 6.5 GBD (Australia). The amount of 0.2 g needles was extracted in 20 mL of 80% acetone. The absorbance of the filtrate was determined for a wavelength of 470 nm (carotenoids), 663.2 nm (chlorophyll *a*), 646.8 nm (chlorophyll *b*) and 750 nm (reference value). The contents of chlorophyll *a* (chl *a*), chlorophyll *b* (chl *b*), total chlorophyll content (chl *a*+*b*), and carotenoids (car *x* + *c*) in µg g⁻¹ of fresh mass were calculated as follows:

chl
$$a = 12.25 \cdot (A_{663.2} - A_{750}) - 2.79 \cdot (A_{646.8} - A_{750}),$$

chl $b = 21.50 \cdot (A_{646.8} - A_{750}) - 5.10 \cdot (A_{663.2} - A_{750}),$
chl $a + b = 7.15 \cdot (A_{663.2} - A_{750}) - 18.71 \cdot (A_{646.8} - A_{750}),$ and
car $x + c = (1000 \cdot (A_{470} - A_{750}) - 1.82 \cdot \text{chl } a - 85.02 \cdot \text{chl } b)/198$

Finally, the 1 g of the fresh needles was dried at 75°C to constant weight (~48 h) to obtain the weight of dry mass and the contents of photosynthesis-related pigments were recalculated to $\mu g g^{-1}$ DW.

Moreover, the ratio between the chlorophylls and carotenoids (chl/car) was calculated.

Fast kinetics of chlorophyll a fluorescence

Polyphasic chlorophyll *a* fluorescence induction kinetics were measured using a fluorimeter HandyPEA (Hansatech Instruments Ltd). Three measurements per tree were conducted. The needles were dark-adapted for 30 min using leaf clips, and subsequently chlorophyll *a* fluorescence was excited by a one-second-long saturation flash with an intensity of 3500 µmol m⁻² s⁻¹. The maximum quantum yield of PSII (F_v/F_m), performance index on absorption basis (PI_{ABS}) and the number of active reaction centres per antenna (RC/ABS) were determined (Strasser *et al.* 2000; Kalaji *et al.* 2014).

Rapid light curves of chlorophyll a fluorescence (RLCs)

RLCs were recorded using a fluorimeter Pam-2500 (Waltz) in three repetitions for six individuals per provenance. Measurements consisted of seven periods of actinic illumination with increasing intensities from 1 to 1659

μmol m⁻² s⁻¹ and a duration of 30 s (the duration of given actinic lights was established experimentally on an unstressed fir, as duration at which the highest values of relative electron transport rate were obtained with maintaining a stable shape of curve). Periods of illumination were separated by 60 ms saturating flashes with the intensity of ~6580 μmol m⁻² s⁻¹. We recorded RLCs for an effective quantum yield of PSII (RLC_{ΦPSII}); non-photochemical quenching of maximal fluorescence (RLC_{NPQ}); and electron transport rate (RLC_{ETR}). The ETR values at a given actinic illumination were calculated as: Φ_{PSII} × PAR × 0.5 × 0.84, where 0.5 is a multiplication factor and 0.84 is the average fraction of absorbed light in the visible range for the many assimilatory organs (Genty *et al.* 1989).

The RLCs were quantified as follows: (i) value records at high light conditions (1659 μ mol e⁻m⁻² s⁻¹) for RLC_{ΦPSII} and RLC_{NPQ} and (ii) maximal electron transport rate, which reflects the light-saturated capacity of the sample, for RLC_{ETR} (ETRmax, μ mol e⁻m⁻² s⁻¹). ETRmax was calculated automatically according to model by Eilers and Peeters (1988) implemented in the machine.

Gas exchange

The open gasometric system Li-6400XT equipped with the standard leaf chamber fitted with 6400–02B LED light source (LI-COR Biosciences) was used for recording the CO₂ assimilation rate (A, µmol CO₂ m⁻² s⁻¹), stomatal conductance (g_s , mol H₂O m⁻² s⁻¹) and transpiration rate (E, mmol H₂O m⁻² s⁻¹). All measurements were carried out on six individuals per provenance on three branches before the appearance of midday depression of photosynthesis. The conditions in the chamber were stable with CO₂ concentration of 400 µmol mol⁻¹, the saturating PAR of 1300 µmol m⁻² s⁻¹, the average block temperature of 22°C and the average RH of 55%, whereas the needles covered whole area of chamber. The adaptation inside of the chamber lasted from 1 to 3 min depending on the speed of stabilisation.

Statistical analyses

Statistical analyses were performed in R 3.1.2 (R Core Team) and Statgraphics Centurion XVI 16.1.11 (StatPoint Technologies Inc.).

The normality of the data distribution was tested before the statistical tests, and transformation was necessary for several parameters. As the block effect was found to be non-significant for most of the tested parameters in a preliminary study, the data from the two blocks were merged. The differences among provenances and between the measurement dates were tested using a two-way ANOVA following the model: $y_{ijk} = date_i + prov_j + date_i \times prov_j + \varepsilon_{ijk}$, where y_{ijk} represents the measured value of the phenotype, date_i is the effect of the *i*th date of measurements, $prov_j$ is the interaction between the date of measurements and the provenance and ε_{ijk} is the experimental error. All effects were considered fixed.

Geographic and climatic clines were investigated using linear models; the individual averages were plotted against geographic and/or basic climate variables of provenance origins. The basic climatic variables were obtained from the WorldClim database with the 30 arc-seconds resolution (Hijmans *et al.* 2005). Moreover, we calculated the Ellenberg's climate quotient (EQ) as the mean temperature of the warmest month/annual precipitation \times 1000 (Ellenberg 1988).

Results

Meteorological characteristics

The mean air temperature of the growing season (April-September) in 2015 was 1.8°C above the long-term mean according to WorldClim (Hijmans et al. 2005), with a 107 mm precipitation deficit (78% of the long-term amount). The temperature in all months of the studied period was above the long-term mean temperature, especially in August (+3.7°C), including heat waves during the summer months (Fig. 2a, b). Although May and June had abundant precipitation, July and especially August were deficient in precipitation (76 and 17% of normal respectively). This resulted in the drying of the soil profile, as expressed by the decrease in soil water potential Ψ soil (Fig. 2c), which decreased from -0.03 to -1.29 MPa between the two measurement dates. Both measurement days (14 July and 4 September, Fig. 2d, e) were colder compared with the previous heat waves with patchy cloudiness. Additionally, light precipitation (showers) occurred during the day and night before both measurement days.

Photosynthesis-related pigment contents

We found slight differences among the provenances related to their photosynthesis-related pigment contents, but significant differences between the measurement dates were recorded only for the chlorophyll/carotenoid ratio (Table 2). The high-altitude provenances AT and SK02 showed aboveaverage values for all tested parameters and did not show significant changes within the growing season (Fig. S1 available as Supplementary Material to this paper). In contrast, the provenance PL41, which originated from the lowest altitude and the driest and warmest location, showed a decline in both pigment types. Moreover, after the stress period, we observed climatic clines that confirmed a significant increase in the total content of chlorophylls with increasing altitude of origin corresponding also to significant clines with increasing precipitation and decreasing temperatures. The content of carotenoids decreased across the latitudinal gradient and the Ellenberg's quotient gradient (Fig. 3).

Chlorophyll a fluorescence

The measurements of fluorescence parameters in darkadapted samples confirmed significant variation both among provenances and between measurement dates (Table 2). We recorded an increase in almost all tested parameters despite the stress period. Similar to the pigment content, the low-altitude provenance PL41, which originated from the warmest and driest conditions, showed the lowest number of reaction centres per antenna (RC/ABS), which also affected the overall PSII performance, expressed as the performance index on absorption basis (PI_{ABS}) and the maximal quantum yield of PSII (F_v/F_m). This was confirmed by the climatic clines (Fig. 3), in which the photochemical performance of PSII increased with increasing altitude and precipitation rate and, on the contrary, declined with the increasing temperature and Ellenberg's quotient at the origin site. The PSII performance increased from south–east to north–west. Most of these trends were consistent on both measurement dates.

The parameters of PSII photochemistry in the light-adapted state varied among the provenances and between measurement dates, except for the effective quantum yield of PSII. However, all PSII photochemistry parameters measured in the lightadapted state were reduced overall by the naturally occurring heat and drought events. The effective quantum yield (Φ_{PSII}) and maximal electron transport rate (ETRmax) were above average in provenances from higher altitudes under non-stressed conditions, and the significant climatic trends confirmed this result. The highest values of the mentioned parameters during July were observed for provenance SK01; however, this provenance showed the greatest declines in Φ_{PSII} and ETRmax after stress (decreases of 12.8 and 24.2% respectively). The ability to dissipate excess energy through non-photochemical quenching (NPQ) was affected negatively and decreased steeply after the stress period in all provenances. However, the provenance SK01 showed the lowest decrease and the highest NPQ ability after the occurrence of natural stress.

Moreover, the individuals that were able to preserve and/or synthesise more photosynthesis-related pigments (increasing chlorophyll/carotenoid ratio, chlorophyll content and/or carotenoid content) maintained a higher PSII performance after stress exposure (Fig. 4; Table 3).

Gas exchange

We found significant differences in the response of gas exchange parameters among provenances and between measurement dates. Stomatal conductance (g_s) and transpiration rate (E) were reduced significantly after stress exposure for all provenances. The lowest decreases in these parameters, only 5 and 20%, respectively, were recorded for SK01; however, both g_s and E were below average in SK01 during the whole growing season. In contrast, the CO₂ assimilation rate (A) increased from July to September. The provenances originating from the upper part of the altitudinal and precipitation range and the lower part of the temperature range showed an overall greater rate of gas exchange. This was confirmed by the significant climatic clines, which were consistent on both measurement dates.

Discussion

According to Blackburn (2007), photosynthesis-related pigment dynamics are strongly correlated with the physiological status of plants and can be used as an indicator of the ability of the plant to acclimate to the environment. We found differences among the provenances related to the contents of photosynthesis-related pigments and significant increases in the chlorophyll/carotenoid ratio after naturally occurring heat and drought. All provenances, except the lowest-altitude one (PL41), enhanced their concentrations of chlorophylls as well as carotenoids, with the highest



Fig. 2. Seasonal dynamics of mean and maximal daily values of air temperature (a), global radiation (b), sum of precipitation and soil water potential (Ψ soil, c) during the growing season 2015. Dashed vertical lines represent measurement days. Daily dynamics of air temperature and vapour pressure deficit (VPD) on 14 July (d) and 4 September (e).

concentrations reached in the provenances originating from the most humid and cool locations. This behaviour corresponds to the results of Villar-Salvador *et al.* (2008), who studied the fitness-related functional traits in *Retama sphaerocarpa* seedlings and observed that the population from the locality with higher precipitation rates and lower air temperatures synthesised more chlorophyll and carotenoids. However, these results contradict those of other studies in which the

chlorophyll content decreased with increasing altitude (Polle *et al.* 1992; Cui *et al.* 2018). The authors assumed that the lower chlorophyll content was due to the greater availability of photosynthetically active radiation at higher altitudes; thus, photochemistry could operate at satisfactory levels with less chlorophyll. However, under high radiation conditions chlorophyll is constantly synthesised and degraded, and accelerating decomposition establishes a balance at a lower

Variable	Provenance			Date			Provenance \times date		Mean July	Mean September	
	df	F	P-value	df	F	P-value	df	F	P-value		
				Phe	otosynthesis-	related pigr	ments				
Chl a+b ($\mu g g^{-1}$)	4	3.24	0.014	1	1.799	0.182	4	1.796	0.132	3.516 ± 1.188	3.690 ± 1.091
Car ($\mu g g^{-1}$)	4	3.177	0.015	1	0.87	0.324	4	2.09	0.084	0.771 ± 0.231	0.798 ± 0.217
Chl/Car	4	1.03	0.393	1	8.355	0.004	4	0.548	0.701	4.508 ± 0.267	4.607 ± 0.197
				Fl	uorescence	of chlorophy	<i>vll</i> a				
$\Phi_{ m PSII}$	4	19.900	< 0.001	1	0.092	0.762	4	1.396	0.237	0.124 ± 0.021	0.119 ± 0.027
NPQ	4	2.592	0.038	1	103.242	< 0.001	4	1.341	0.257	1.633 ± 0.421	0.986 ± 0.453
ETRmax (μ mol e ⁻ m ⁻² s ⁻¹)	4	20.827	< 0.001	1	14.837	< 0.001	4	5.565	< 0.001	112.89 ± 24.87	101.72 ± 23.80
$F_{\rm v}/F_{\rm m}$	4	8.926	< 0.001	1	5.962	0.016	4	3.358	0.011	0.856 ± 0.024	0.850 ± 0.013
RC/ABS	4	14.022	< 0.001	1	80.722	< 0.001	4	0.644	0.632	1.104 ± 0.215	1.449 ± 0.347
PI	4	11.87	< 0.001	1	14.5	< 0.001	4	0.95	0.437	4.130 ± 1.442	4.962 ± 1.804
					Gas ex	xchange					
$A \;(\mu mol \; CO_2 \; m^{-2} \; s^{-1})$	4	10.085	< 0.001	1	24.011	< 0.001	4	1.675	0.158	7.130 ± 1.276	8.053 ± 1.493
$E \text{ (mmol H}_2\text{O m}^{-2} \text{ s}^{-1}\text{)}$	4	16.27	< 0.001	1	185.29	< 0.001	4	90.03	< 0.001	1.946 ± 0.517	1.403 ± 0.466
$g_{\rm s} \ ({\rm mol} \ {\rm H_2O} \ {\rm m^{-2}} \ {\rm s^{-1}})$	4	21.43	< 0.001	1	60.30	< 0.001	4	37.80	< 0.001	0.156 ± 0.050	0.120 ± 0.039

 Table 2. Analysis of variance for all evaluated parameters

 Means \pm s.d. are displayed for both measurement dates separately. Abbreviations: df, degrees of freedom; *F*, *F*-statistic

July September gs *** *** Е А ** * *** *** *** *** Physiological parameter RC/ABS *** ** *** *** Pearson ΡI *** *** correlation 1.0 Fv/Fm *** 0.5 ** **ETRmax** ** 0.0 NPQ -0.5 -10 Φ_{PSII} chl/car car x+c chl a+B T_{mean} T_{mean} Pyear P_{59} Pyear 59 ЮШ long lat T₅₉ ğ aļt ond <u>a</u>t Ъ 20 alt Climatic variable

Fig. 3. Regression matrices of physiological parameters and climatic variables of provenance origins at the tree level (n = 30) for both measurement dates separately. Significant relationships are indicated: *, P < 0.05; **, P < 0.01; ***, P < 0.001.

chlorophyll concentration (Tan *et al.* 2000). This increases the demand for carotenoids, which contribute to the removal of the accumulated reactive oxygen species to prevent photooxidative damage to the chloroplasts and slow down the chlorophyll degradation (Björkman and Demmig-Adams 1995). Therefore, the increase in carotenoid content in high-altitude provenances may result in increased chlorophyll content as well. We also confirmed this behaviour by identifying significant clines along the precipitation and

temperature gradient, however, these clines formed just at the end of the growing season. Ottander *et al.* (1995) suggested that conifers are able to downregulate their PSII during the winter by partially reducing the amount of chlorophyll and reorganising the LHC into large aggregates to prevent the destruction of thylakoids; therefore, this behaviour could be associated with phenologically postponed recovery of PSII after winter in high-altitude



Fig. 4. Relationships between the chlorophyll *a* fluorescence and the weight ratio of total chlorophylls to carotenoids before (July; open circles) and after (September; closed circles) the natural stress period at the tree level (n = 30). Significant relationships are indicated: *, P < 0.05; **, P < 0.01; ***, P < 0.001.

Table 3.	Correlations between the chlorophyll a fluorescence and the content of photosynthesis-related pigments
	for both measurement dates separately at the tree level $(n = 30)$

Significant correlations are indicated in bold. Abbreviations: NPQ, non-photochemical quenching; ETRmax; maximum electron transport rate; PI, performance index; RC/ABS, number of active reaction centres per antenna

		$\Phi_{ m PSII}$	NPQ	ETRmax (μ mol e ⁻ m ⁻² s ⁻¹)	PI	RC/ABS	$F_{\rm v}/F_{\rm m}$
July	Chl/Car	0.353	0.124	0.253	-0.098	-0.101	-0.320
	Car $x+c$ (µg g ⁻¹)	0.429	0.277	0.300	-0.035	-0.096	-0.349
	Chl $a+b$ (µg g ⁻¹)	0.442	0.240	0.298	-0.053	-0.114	-0.353
September	Chl/Car	0.516	-0.103	0.620	0.474	0.456	0.144
	Car $x+c$ (μ g g ⁻¹)	0.310	0.154	0.255	0.543	0.513	0.306
	Chl $a+b$ (μ g g ⁻¹)	0.378	0.156	0.354	0.593	0.568	0.317

provenances as an adaptive mechanism to the later onset of the growing season.

Moreover, we revealed a strong correlation between the maximal photochemical efficiency and the carotenoid content at the end of the growing season after natural heat and drought, supporting the assumption that individuals, which accumulate more photosynthesis-related pigments are able to maintain higher photochemical performance and are less susceptible to combined moderate heat and drought.

The photochemical efficiency in the dark-adapted state was overall higher for high-altitude provenances, as confirmed by several geographical and climatic trends. In a study of the PSII thermotolerance of 17 silver fir provenances growing in the same experimental plot (Hertník) and in another experimental plot (Kaprun), including provenances from both Central European and Balkan refugia, the same climatic trends for the Central European provenances were observed. The Balkan provenances were able to withstand the highest temperatures, probably as a result of their adaptation to the overall warmer climate at their sites of origin. However, the behaviour of several provenances was inconsistent and differed based on the conditions of the plantation sites, so they stated that silver fir showed a relatively high ability to acclimate its PSII performance to the current growing conditions (Konôpková *et al.* 2018).

The results for the light-adapted samples were not as consistent; the lowest PSII performance was recorded in provenance PL21, which originated from middle altitudes, and slightly increased towards the range margins. Nonphotochemical quenching was also the lowest in provenance PL21 and was above average in provenances SK01 and highaltitude provenances SK02 and AT, reflecting their ability to mitigate adverse stress effects at the chloroplast level through the heat-dissipation of excess light energy (Hazrati et al. 2016). However, the maximal quantum yield, effective quantum yield, electron transport rate, and nonphotochemical quenching were significantly reduced after the combined drought and heat. This reduction probably resulted from the heat rather than the drought because primary photochemical stage is highly affected by high temperatures but quite resistant to water deficits (Shah and Paulsen 2003). Under heat stress, the reduction of photosynthesis is first attributed to reduced PSII activity as a result of structural alterations of chloroplast proteins D1 and D2, decreased enzymatic activity, and damaged thylakoid membrane and the oxygen-evolving complex; the degradation of photosynthesis-related pigments may also play a role in the decline in photosynthesis (Haldimann and Feller 2004; Zhang et al. 2005). However, in our study, the degradation of photosynthesis-related pigments was certainly excluded as a result of the lower photosynthetic rates and furthermore, we observed increasing number of active RCs and the performance index on absorption basis. This indicates the ability of different provenances of silver fir to make shortterm adjustments in their photosynthesis-related pigments and thereby also to adjust their photochemical activity (Havaux 1993). Peguero-Pina et al. (2007) also confirmed the different long-term photochemical responses of two silver fir populations from geographically close but climatically contrasting localities in the Spanish Pyrenees. The population growing at a higher altitude with a higher precipitation rate and lower annual temperatures showed a higher photochemical efficiency, heat dissipation ability and photosynthetic rate, as indicated by gas-exchange parameters.

We also observed significant climatic clines across altitudinal, precipitation and temperature gradients for CO₂ assimilation rate, stomatal conductance, and transpiration rate on both measurement days. Although stomatal conductance and transpiration rate were reduced by approximately onethird after the moderate drought and heat, the photosynthetic rate overall increased, especially in provenance AT. This indicates that provenance AT showed the highest ability to optimise the overall amount of water lost through transpiration versus biomass accumulation under limited water conditions and thus had the highest water usage efficiency (Kruse et al. 2012). Such behaviour has been described in various other species, e.g. European beech (Bresson et al. 2011; Pšidová et al. 2015; Kučerová et al. 2018), sessile oak (Bresson et al. 2011), and Merkus pine (Koskela 2001), which suggests that the relatively high level of photosynthetic performance of high-altitude provenances is a genetically determined adaptive mechanism for compensating of the extreme weather and the short growing season in these localities.

The physiological mechanisms behind this advantage might be achieved by ability to accumulate more nitrogen, as was confirmed for high-altitude provenances of Norway spruce (Oleksyn *et al.* 1998). Higher content of nitrogen generally leads to higher Rubisco content (Li *et al.* 2013) influencing overall assimilation rate.

However, because of the high daily temperature amplitude and strong solar radiation at high altitudes, these provenances may also require stronger photoprotective mechanisms (Chaves et al. 2003; García-Plazaola et al. 2015), such as (i) non-photochemical quenching, (ii) reactive oxygen species scavenging, (iii) production and emission of volatiles, (iv) synthesis of heat-shock proteins and/or (v) osmotic adjustment through the accumulation of osmolytes. Osmolytes may increase turgor and thus increase stomatal conductance, photosynthetic rate and the possibility of transpirationmediated cooling and may also protect cellular structures and stabilise membranes by buffering the redox potential of the cell. Moreover, the previously mentioned carotenoids are involved in photoprotection and simultaneously are the precursors for the synthesis of abscisic acid. Therefore, upregulated photoprotective mechanisms can provide them an advantage under various other elementary stresses, not just under high-light conditions (Allakhverdiev and Murata 2004; Allakhverdiev et al. 2008; Junker et al. 2017).

In this context, we are aware that the differences between provenances could result from both genetic adaptation and environmental acclimation, and the changes between the measurement dates could be influenced not only by heat and drought but also by natural seasonal dynamics in pigment concentration (phenology). Regardless, the observed clines are consistent between measurement dates and with the comparable slope for most assessed traits. Therefore, we may conclude that the Central European provenances originating from higher altitudes, i.e. wetter and colder conditions, showed overall higher photochemical performance under suboptimal growing conditions (as the Hertník plot is located below the optimal fir climate conditions) and were less prone to the naturally occurring heat and drought. These results might be surprising as some studies suggest that provenances originating from dry and warm sites are more resistant to drought (Pšidová et al. 2015; Hajek et al. 2016; Stojnić et al. 2018). In contrast, Pšidová et al. (2018) confirmed lower resistance of PSII (based on electron transport at the PSII acceptor side and the size of light harvesting complexes) for beech originating from lower altitudes, assuming lower phenotypic plasticity of those. It is also possible that trees originating from lower altitudes are more responsive to moderate stress but are under lower thread under extreme drought as lower growth may indicate readjustments in carbon allocation and thus better survivability (Chuste et al. 2020). Similarly, Jamnická et al. (2019) described that the mountain environment leads to the adoption of a 'riskier strategy' to cope with suboptimal water supply, i.e. synthesising more osmolytes and thus maintaining significantly higher photosynthetic performance. On the contrary, the provenances from lower altitudes adopt a 'conservation strategy', i.e. accumulating more abscisic acid and thus closing the stomata faster, which limits the CO₂ assimilation rate as well. Therefore, we suggest that the local adaptation to the climatic conditions at the provenance origin site makes a large contribution to silver fir photosynthetic performance. Of course, there are sources of uncertainty and generalisation of obtained results might be problematic as trends might be valid for the particular soil (Buras et al. 2020) and climatic conditions, but not for all others plots. For example, Kurjak et al. (2019) observed much more pronounced differences in thermostability of PSII among beech provenances growing at a warmer plot compared with a colder one. Wortemann et al. (2011) confirmed the significant effect of the site on cavitation resistance of beech but found no significant differences across populations. Contradicting this result, Stojnić et al. (2018) confirmed differences between populations of beech originating from geographically marginal sites. There are also another problematic aspects of the provenance research, mainly extrapolation of the measurements performed on young trees to the age of rotation (Gömöry et al. 2020) and this is even bigger issue for short-term controlled experiments. Nevertheless, provenance trials remain one of the most powerful tool for predicting the response of tree species to expected climatic conditions.

Conclusion

Our results showed that the low-altitude provenances originating from dry, hot localities had weaker photosynthetic performance and higher responsiveness to moderate stress exposure than the high-altitude provenances. This confirmed our hypothesis that the distinct provenances are characterised by different photosynthetic responses as a result of their long-term adaptation to environmental conditions at the provenance origin site. However, it is still an open question whether the lower responsiveness of high-altitude provenances to moderate stress and their efforts to maintain high photosynthetic performance under suboptimal conditions provide an advantage under long-lasting or more severe stress as well.

We assume that the use of advanced physiological approaches has great potential for forestry purposes whereas the better understanding of particular processes may lead to an adjustment of legislation restricting the transfer of reproductive materials. Moreover, this knowledge may serve as a guide for future studies, including association studies to reveal the genetic background of adaptation-related traits, and may provide valuable information for process-based modelling of forest growth and productivity. However, we are far from a detailed understanding of the physiological processes behind the production or vitality. Comparisons of populations growing at contrasting plots and thorough comparison of the most important forest tree species remains one of the challenges for the future research.

Conflicts of interest

The authors declare no conflicts of interest.

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