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Photosynthetic response of beech seedlings of different origin to water deficit

E. PŠIDOVÁ[*,+], Ľ. DITMAROVÁ[*], G. JAMNICKÁ[*], D. KURJAK[**,***], J. MAJEROVÁ[*],
T. CZAJKOWSKI[#], and A. BOLTE[#]

Institute of Forest Ecology, Slovak Academy of Sciences, 960 53 Zvolen, Slovak Republic[*]
Faculty of Forestry, Technical University Zvolen, 960 53, Zvolen, Slovak Republic[**]
Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, 165 21, Prague 6, Czech Republic[***]
Thünen Institute of Forest Ecosystems, 16225, Eberswalde, Germany[#]

Abstract

European beech (*Fagus sylvatica* L.) seedlings of three different origins were used to evaluate the effect of water deficit and recovery during the most vulnerable phase of forest tree life. Gas-exchange characteristics and fluorescence rapid light curves were studied in the seedlings from a warm region (PV1, 530 m a.s.l.), seedlings from a moderately warm region (PV2, 625 m a.s.l.), optimal for beech, and in seedlings from a cool region (PV3; 1,250 m a.s.l.). Changes in photosynthetic characteristics caused by water deficit were similar, but their intensity was dependent on the origin of the seedlings. Simulation of drought conditions by the interruption of watering led to a decrease in the efficiency of primary photochemistry in PSII, with the most significant decrease in the PV2 seedlings. Conversely, water deficit affected most significantly gas exchange in PV3, where the recovery process was also the worst. The PV1 demonstrated the highest resistance to water deficit. Drought-adaptation of beech seedlings at non-native sites seems to be linked to water availability and to the origin of the beech seedlings.

Additional keywords: chlorophyll *a* fluorescence; leaf water potential; net photosynthetic rate; photosynthesis; stomatal conductance; water-use efficiency, provenances, *Fagus sylvatica*.

Introduction

The current frequency and intensity of extreme drought events across Europe is greater than in the past; thus, the ability of trees to recover from drought damage and to survive periods of drought attracts increased attention (Galle and Feller 2007). In recent decades, an increasing frequency of warming during the spring and a subsequent increase in the occurrence of dry periods in the summer has been observed. Precipitation deficits in the winter and early spring result in poor water supplies which subsequently causes water deficit during the vegetation period (Welp *et al.* 2007, Allen *et al.* 2010). Sufficient moisture in the spring represents one of the main conditions for germination and survival of beech seedlings (Barna and Jarčuška 2011). Investigation of the beech seedling survival at forest sites confirmed that the highest mortality is during the first year, while the first five years are the most critical in terms of survival (Szwagrzyk *et al.* 2001, Valladares *et al.* 2002, Agestam *et al.* 2003, Barna 2011, Repáč *et al.* 2011).

Water deficit, the most common and natural environmental limitation, is a factor controlling the production and distribution of the European beech (Silva *et al.* 2012). Its growth and competition abilities may be strongly influenced by intense drought effects (Geßler *et al.* 2007). The development phase of seedlings is known as the most vulnerable phase of forest tree life; therefore, understanding the stress responses of the seedlings is crucial for the prediction of forest tree growth and survival

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[+]Corresponding author; phone: 00421 45 533 0914, fax: 00421 45 547 9485, e-mail: evkapsidova@yahoo.com, psidova@sav.savzv.sk

Abbreviations: C – control; DS – drought stress; F_m' – maximum fluorescence yield of a light-adapted leaf; F_v'/F_m' – maximum efficiency of open PSII reaction centre in the light; g_s – stomatal conductance; NPQ – nonphotochemical quenching; P_N – net photosynthetic rate; PV1 – warm region; PV2 – moderately warm region; PV3 – cool region; rETR – relative electron transport rate; Q_A – primary quinone acceptor of PSII; q_N – coefficient of nonphotochemical quenching; q_P – coefficient of photochemical quenching; R – recovery; RLC – rapid light curve; WUE_i – intrinsic water-use efficiency (= P_N/g_s); $\Delta F/F_m'$ – effective quantum yield of PSII under light; Φ_{PSII} – effective quantum yield of PSII; ψ_{pd} – predawn leaf water potential.

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(Padilla *et al.* 2007, Niinemets 2010).

Beech forests have been mainly grown by natural regeneration, and their provenances developed through adaptation to local climatic conditions (Müller-Stark 1997). The expected prolonged and frequent summer drought periods may affect water regime, nutrient uptake, growth, fitness, and interactions of beech with other organisms, especially in soils with low capacity for water retention (Geßler *et al.* 2007). In the context of climate change, information regarding beech provenances tolerant to drought becomes notably important, particularly for forest management and future reforestation. In seedling studies and experiments, eastern and southern provenances were found to be more drought-adapted (Czajkowski *et al.* 2005, Czajkowski and Bolte 2006, Rose *et al.* 2009, Thiel *et al.* 2014). This finding can be explained by the evolutionary adaptation of beech at the xeric 'rear edge' of its distribution under high selection pressure from frequent and intensive drought events (Hampe and Petit 2005, Bolte *et al.* 2007). Provenance research trials in forest science has been limited to experimental work to date; many of them were organised by IUFRO through extensive international cooperation. These experiments have contributed to the identification of trends in phenotypical traits of commercially significant species over its entire distribution area. Recently, the paradigm has been shifted, especially in the context of climate change, toward the direct assessment of adaptability with the implementation of ecophysiological research methods (Gömöry *et al.* 2010).

Drought has a substantial influence on basic physiological processes in trees, primarily the photosynthetic assimilation of CO_2, stomata closure, transpiration, *etc*. In seedlings, the storage carbon pool size is relatively small and a reduction in the net assimilation rate leads to the fast depletion of the reserves for plant maintenance processes, further strengthening the stress effect on the plant (Niinemets 2010). The efficient photosynthetic process and a functional photosynthetic apparatus are necessary for plant growth and biomass production. Under mild stress, a small decline in stomatal conductance (g_s) may protect plants from stress by improving plant water-use efficiency (WUE_i) (Chaves *et al.* 2009). WUE_i is an important indicator for evaluating drought resistance and is a key plant trait linking the terrestrial carbon and water cycles (Yin *et al.* 2005, Barbour *et al.* 2011).

PSII was recognised as the most vulnerable component of the photosynthetic apparatus because it is highly sensitive to light damage. This property can also be useful as an indicator of stress, because the impairment of PSII is frequently the earliest sign of stress in leaves (Maxwell and Johnson 2000).

Rapid light curves (RLC) of chlorophyll (Chl) *a* fluorescence provide detailed information regarding the saturation characteristics of electron transport, as well as the overall photosynthetic performance of the plant. We explored how to use best this property of RLCs (Ralph and Gademann 2005). In comparison with traditional light curves, the RLC measures the effective quantum yield of PSII (Φ_{PSII}) as a function of irradiance; however, the RLC does not require to reach steady-state conditions during each light step (Schreiber *et al.* 1997). RLCs use only 10 s of actinic light at each of the eight light steps, and the Φ_{PSII} and relative electron transport rate (rETR) indicate the actual state of photosynthesis. This is in contrasts with steady-state light curves, which are independent of the light history and indicate the optimal state of photosynthesis. In general, the measurement of RLC elucidates the characteristics that are independent of the current ambient light conditions but are based on leaf ontogeny and on the range of physiological plasticity of the plant (Rascher *et al.* 2000).

The research on responses to changing environments commonly uses the parameters of Chl fluorescence rapid kinetics in forest woody plants. These parameters, however, are believed to indicate relatively high resistance against drought (Ögren 1990, Tognetti *et al.* 1995, Ritchie 2006, Roostaei *et al.* 2011).

The primary objective of this study was to identify changes in photosynthesis, fluorescence RLCs, gas exchange, and WUE_i during the water deficit and recovery cycle in *F. sylvatica* seedlings from different regions of Slovakia. We aimed to determine the drought response and water-deficit tolerance in relationship with the plant origin. We wanted to test the hypothesis that the beech originating from a relatively xeric site is more water deficit–tolerant than that from more humid sites. Such information may be useful for improving breeding strategies and forest management (Millar *et al.* 2007).

Materials and methods

Plants and experimental design: The experiment was performed under controlled water availability, air temperature, and humidity. The experiment lasted 10 d and started with control (C) measurements. Then, the water supply was interrupted to simulate water stress (DS). The drought period lasted for seven days (from 7 to 13 August). After this period, the seedlings were watered for three days (from 14 to 16 August), and their recovery (R) was monitored. The plant material was provided by the nursery centre Drakšiar (Beňuš, Slovakia). Each provenance was represented by four plastic boxes (140 seedlings). Seeds of *Fagus sylvatica* L. were collected at a specialised factory in Slovakia (*Lesy SR s.p.*, *OZ Semenoles* in Liptovský Hrádok), which provided the collection, processing, storage, and sale of forest tree seeds in different geographical areas. Seeds representing provenance PV1 were collected in Divín (48°33'N, 19°36'E), a warm region with 50 or more summer days on average annually (with the daily maximum air temperature ≥ 25°C). The seeds representing provenance PV2 were from Dobšiná (48°49'N, 20°18'E), a moderately warm region with less than 50 summer days on average annually (with the daily maximum air temperature ≥ 25°C and the July mean temperature ≥ 16°C). The seeds representing provenance PV3 were collected in Pohorelá (48°54'N, 19°56'E), a cool region with the July mean temperature < 16°C, all subregions in this region are considered to be highly humid (Table 1). Storage and seedbed preparation were carried out in a nursery centre, Drakšiar. The one-year-old seedlings were grown in plastic boxes (35 containers), each containing 200 ml of universal soil substrate of peat and composted bark (*Kera U*).

The experiment was carried out in a climate-controlled chamber under the following conditions: temperature of 23–23.5°C; relative air humidity of 65%; 12-h light period by using four high-pressure discharge tubes *LU400PSL/T/E40* (*General Electric*, USA) providing the irradiance of 610 µmol(photon) m^{-2} s^{-1} .

Soil water content was measured by the gravimetric method using the *KERN FKB 15KO.5A* scale (*KERN & Sohn GmbH*, Germany) with sensitivity of d = 0.5 g. We weighed each plastic box with 35 beech seedlings during three treatments (C, DS, R).

Predawn leaf water potential (ψ_{pd}) was determined psychrometrically using a *PSYPRO* (*Wescor*, USA), which comprises a chamber equipped with thermocouples. In our experiment, we used a psychrometric chamber *C-52*, where leaf discs with a diameter of 1 cm were inserted. The ψ_{pd} was measured for three days (August 7, 13, and 16) 1 h before the start of the daily light regime. On each day, four samples of each provenance (PV1, PV2, and PV3) were measured.

Leaf gas-exchange measurements were performed with an *LI–6400XT* (*LI-COR*, USA) portable photosynthesis measuring system. P_N and g_s were monitored three times during the experiment on ten fully expanded leaves (one leaf each from ten seedlings) per each provenance. The CO_2 concentration in the chamber was 390 µmol m^{-1}, the irradiance was 1,200 µmol(photon) m^{-2} s^{-1}, and the average temperature was 23°C. WUE_i was calculated as the ratio of P_N and g_s.

Chl fluorescence was measured with a *MINI-PAM Fluorometer* (*Walz GmbH*, Germany). The sample seedlings were removed from the climatic chamber and placed in the shade [20–30 µmol(photon) m^{-2} s^{-1}] for 30 min before the measurements. The measurements were done with the same sample leaves during the whole experiment and ten leaves (one leaf from each ten seedlings) per provenance were used. RLCs were measured automatically under the control of an internal program in which the actinic illumination was applied in eight steps, with light intensities increasing from 24 to 367 µmol(photon) m^{-2} s^{-1}. Each illumination period lasted 10 s and was separated by a 0.8-s saturating flash from a white halogen lamp [2,000–3,000 µmol(photon) m^{-2} s^{-1}]. Before the first saturating pulse of the RLC, an initial quasi-darkness measurement was taken to estimate the F_v'/F_m' ratios related to the quantum yield of the ambient light state of the sample. Quasi-darkness (5–10 s) allows the rapid reoxidation of the primary electron acceptor (Q_A) without substantial relaxation of the nonphotochemical quenching coefficient (Schreiber 2004, Ralph and Gademann 2005).

The *MINI–PAM* records all relevant fluorescence parameters: the effective quantum yield of PSII ($\Phi_{PSII} = \Delta F/F_m'$); electron transport rate (ETR) values at a given actinic irradiance, PAR ($ETR = \Phi_{PSII} \times PAR \times 0.5 \times 0.84$), where 0.5 is a multiplication factor for two quanta of light required for the transport of one electron, and 0.84 is the species-specific fraction of incident quanta absorbed by the leaf; coefficient of photochemical quenching (q_P); coefficient of nonphotochemical quenching (q_N), and a parameter describing nonphotochemical quenching (NPQ) assuming a matrix model of the antenna system based on Stern–Volmer quenching.

Table 1. Geographical and climatic characteristics of the studied beech provenances (Landscape Atlas of the Slovak Republic 2002). The data represent 30-year averages (1980–2010) and were calculated from surrounding places.

Parameter	PV1	PV2	PV3
Altitude [m a. s. l.]	530	625	1,250
Climatic region	warm	moderately warm	cool
Subregion	warm, dry, with cool winter	moderately warm, very humid, highlands	moderately cool
Mean annual air temperature [°C]	9.2	8.9	5.1
Mean annual minimum air temperature [°C]	4.0	3.9	1.1
Mean annual maximum air temperature [°C]	14.8	14.3	10.2
Mean temperature for the growing season [°C]	16.2	16.0	11.3
Mean annual rainfall [mm]	595.7	693.3	884.8
Subsoil	granodiorite	phyllite	gneiss
Type of soil	cambisoil	cambisoil	humic podzols

Data analysis: The data obtained in the experiment were processed statistically with the programme *Statistica 7* (*Statsoft,* USA). The significance of differences between the treatments and provenances was tested with an analysis of variance (*ANOVA*) and *Duncan*'s post-hoc test with $P<0.05$ considered to be significant. During the drought treatment, one seedling of PV3 died. During the recovery period, additional seedlings from groups of PV2 and PV3 died, and the seedling numbers in these provenances were reduced to seven (PV2) and six (PV3).

Results

Soil water content: Changes in the average mass are shown in Fig. 1.

Predawn leaf water potential: The water deficit decreased significantly ψ_{pd} in all of the considered provenances (Fig. 2). The reduction was most significant in PV1 with a decrease from –0.38 MPa to –1.82 MPa. None of the studied provenances fully recovered the original ψ_{pd} within the three days of recovery. *ANOVA* showed a partial recovery only in PV2, which increased its ψ_{pd} from –1.74 MPa to –1.17 MPa.

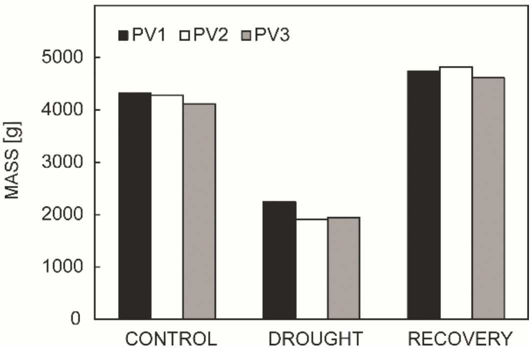

Fig. 1. Changes in soil water content expressed as average mass of boxes containing 35 beech seedlings from 3 selected provenances (PV1, PV2, and PV3) in conditions of control, drought, and recovery.

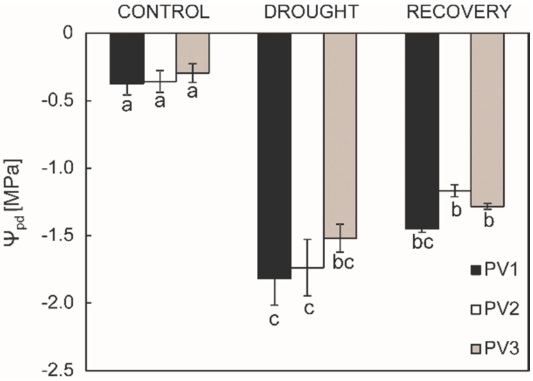

Fig. 2. Changes in leaf water potential (ψ_{pd}) in leaves of beech seedlings from three selected provenances (PV1, PV2, and PV3) in conditions of control, drought, and recovery. The data are presented as the mean values ± SE. $n = 4$. *Small letters* indicate statistically significant differences ($P<0.05$) between treatments and provenances.

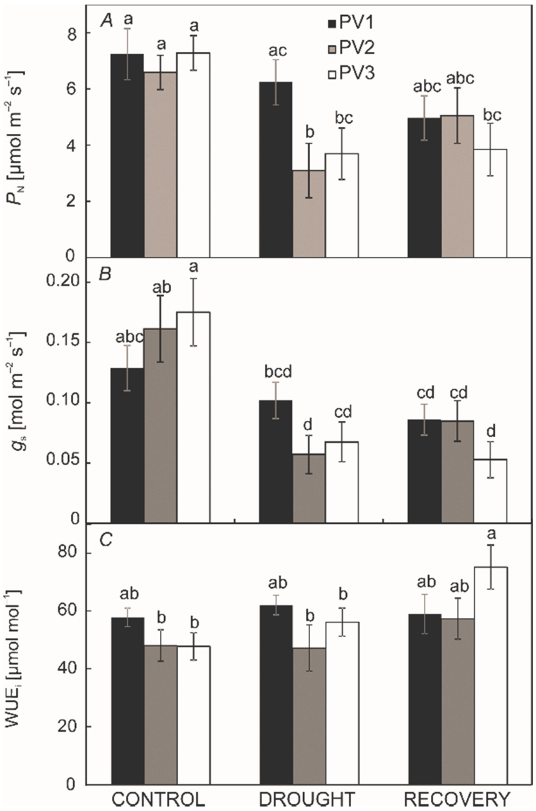

Fig. 3. Changes in P_N (*A*), g_s (*B*), and WUE_i (*C*) in leaves of beech seedlings from three selected provenances (PV1, PV2, and PV3) in conditions of control, drought, and recovery. The data are presented as the mean values ± SE. $n = 10$. *Small letters* indicate statistically significant differences ($P<0.05$) between treatments and provenances.

Leaf gas exchange: We found statistically significant reductions in the P_N and g_s in PV2 and PV3 due to the water deficit. The WUE_i did not vary significantly, except for the increase in PV3 during recovery. The seedlings from PV3 manifested the highest mortality (four out of ten); the moderate, statistically insignificant decrease in g_s in the surviving PV3 seedlings resulted in a significant increase in WUE_i compared with the previous measurements. The smallest impacts of the DS and R phases were manifested in PV1. The PV2 was the only provenance to show both a clear response to DS and a moderate increases in P_N and g_s during the R phase. Although the water deficit response was also apparent in PV3, this provenance exhibited a distinct mortality and no positive changes in the P_N and g_s values during the R phase (Fig. 3*A, B*).

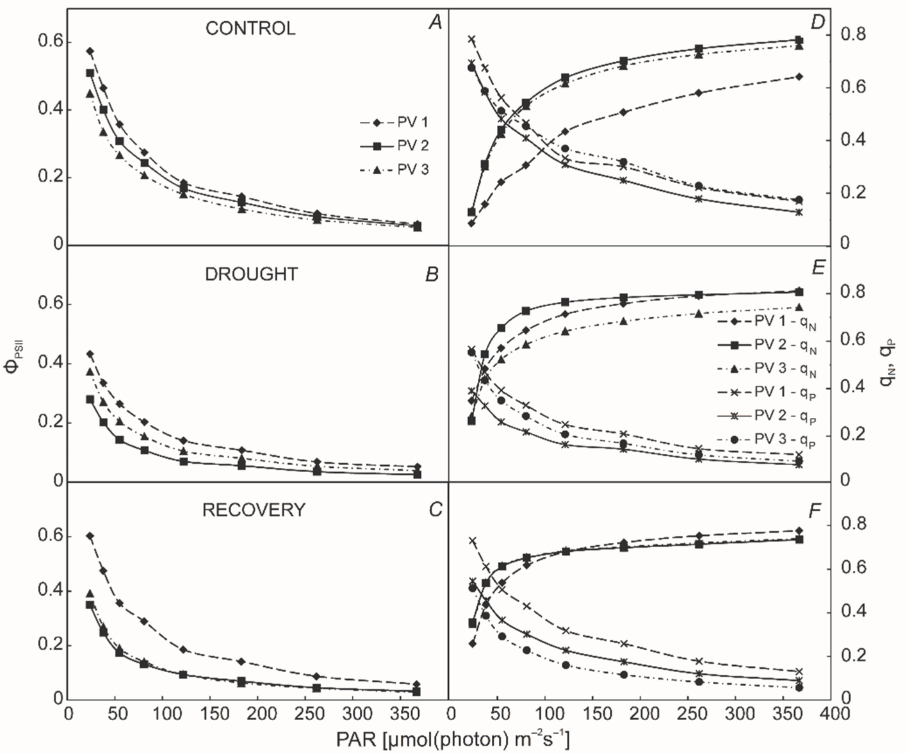

Fig 4. Changes in rapid light curves (RLCs) for Φ_{PSII} in leaves of beech seedlings from three selected provenances (PV1, PV2, and PV3) in conditions of control (*A*), drought (*B*), and recovery (*C*). Changes in RLCs for q_P and q_N in leaves of beech seedlings from these provenances (PV1, PV2, and PV3) in conditions of control (*D*), drought (*E*), and recovery (*F*). The data are presented as the means. *n* = 10. q_N – coefficient of nonphotochemical quenching; q_P – coefficient of photochemical quenching; Φ_{PSII} – effective quantum yield.

Chl fluorescence: Initially, control treatment values of Φ_{PSII} were within 0.45–0.57 (Fig. 4*A*) and the values of q_P ranged from 0.68–0.78 for all seedlings (Fig. 4*D*). The water deficit decreased Φ_{PSII} and q_P of the PV1 seedlings due to increased energy loss *via* nonphotochemical quenching (significant increase in NPQ and q_N). At the same time, the Φ_{PSII} and q_P of the PV2 seedlings dropped markedly because of the lower capacity for nonphotochemical energy dissipation (Fig. 4*B*,*E*). The recovery capacity was the best for q_P of PV1. In contrast, the PV3 seedlings manifested a decreasing trend in their q_P values, even after three days of the R phase, and their q_P value was approximately 0.057 at the end of the light period.

The greatest ability of the photosystems to utilise absorbed light energy under DS was observed in the PV3 seedlings, where only a small portion of light energy was converted to heat. However, a conspicuous improvement in dissipating the excess light was found in PV1 and PV2 (Fig. 5*B*). The trends in RLCs NPQ under the recovery treatment were parallel in all studied provenances.

The RLC–ETR (recovery treatment) values in PV1 and PV2 indicated a reduced portion of light energy converted to heat. However, for PV3, which showed the best resistance to DS, the RLC–ETR values did not indicate a discernible recovery (Fig. 5*F*). The rising part of the slope at the beginning of the RLC–ETR (control treatment, C) showed the highest efficiency of light harvesting by beech seedlings from PV1 and lower efficiencies for PV2 and PV3 (Fig. 5*D*). Under DS, conspicuous changes occurred in the rising part of the slope, especially in PV2, which showed the most remarkable reduction. None of the studied provenances exhibited a decreasing slope at the end of the RLC–ETR. Consequently, we assumed that the water deficit did not cause photoinhibition (Fig. 5*E*). The rewatering exhibited the greatest positive impact on seedlings from PV1 (Fig. 5*F*).

Discussion

Our study was based on the principle of adaptability assessment. For rapid stress detection (water deficit) and comparisons among the studied beech provenances, we used ecophysiological parameters (ψ_{pd}, leaf gas exchange, Chl fluorescence, and RLCs). These methods demonstrated that drought conditions induce a complex of mutually interconnected and precisely regulated photoprotective responses (Zivcak *et al.* 2013).

The drought treatment and the actual water deficit incidence during the experiment were documented by the measurements of ψ_{pd}. Toward the end of the 7-d water-deficit period, we did not observe significant differences among the provenances, but the decrease in ψ_{pd} was noticeable in all provenances and even below –1.5 MPa. Similar significant reductions of ψ_{pd} were recorded in other beech provenances for seedlings by Rose *et al.* (2009) and in saplings by Galle and Feller (2007). However, contrasting responses have been reported from other beech

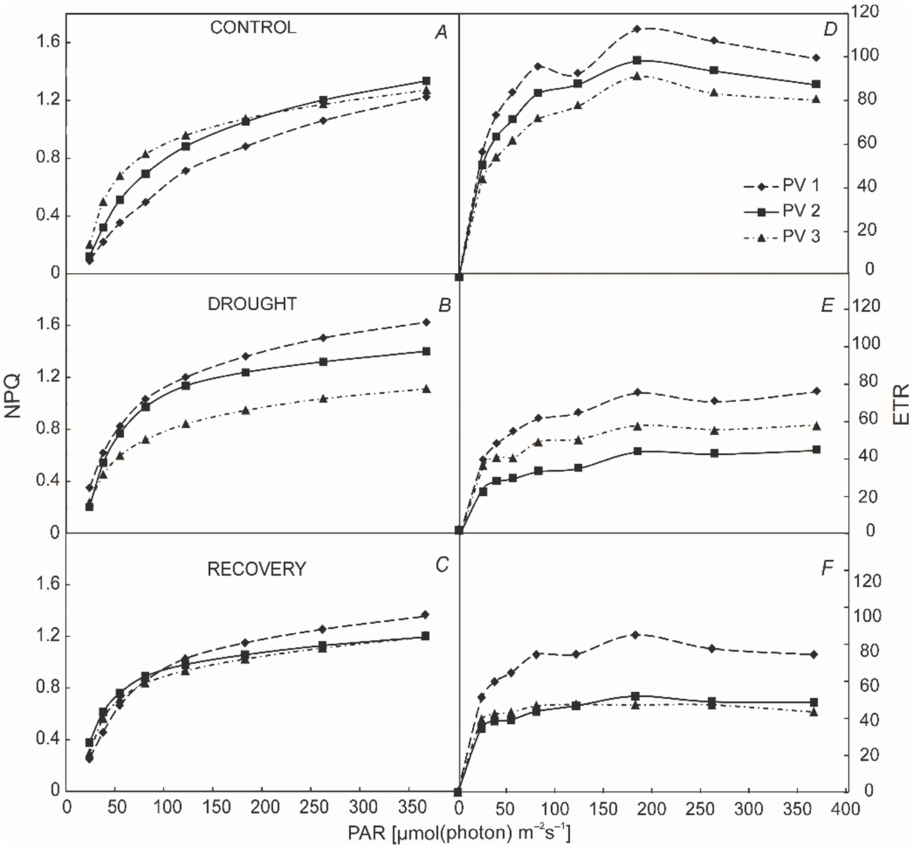

Fig. 5. Changes in rapid light curves (RLCs) for NPQ in leaves of beech seedlings from three selected provenances (PV1, PV2, and PV3) in conditions of control (*A*), drought (*B*), and recovery (*C*). Changes in RLCs for ETR in leaves of beech seedlings from these provenances (PV1, PV2, and PV3) in conditions of control (*D*), drought (*E*), and recovery (*F*). The data are presented as the means. *n* = 10. ETR – electron transport rate; NPQ – nonphotochemical quenching

provenances (Czajkowski and Bolte 2006), especially from Spanish beech forests, for which García-Plazaola and Becerril (2000) observed distinct differences in ψ_{pd} values among seedlings from three beech provenances stressed by dehydration lasting for six days. The authors observed the steepest drop in ψ_{pd} in beech seedlings from the provenance Altube, originating at 300–600 m a.s.l. and from a cool and humid climate with a good water supply. Analogously, in our experiment, the most pronounced decrease was obtained for PV1, originating from 530 m a.s.l., but this response did not significantly differ from the PV2 and PV3. We inferred that the observed recovery of ψ_{pd} after three days of watering was due to a change in root hydraulic conductance (K_R). Gullo *et al.* (1998) tested the response in *Olea oleaster* seedlings and observed an increase in K_R at 48–72 h after irrigation depending on drought severity. Severe drought stress led even to anatomical changes of roots and recovery in these roots required resumed growth of root tips and emergence of new lateral roots.

Naturally, the watering interruption entailed, in addition to the decrease in ψ_{pd}, a significant reduction in the leaf gas-exchange parameters. Variance in P_N among monitored seedlings from different provenances were recorded throughout the course of the experiment. The stomata dehydration effects, stomata closure, and the drop of P_N and g_s, were recorded in PV2 and PV3. The bigger of variance changes were observed in g_s and in WUE_i, however, we recorded the only small variance among the studied provenances.

The stomatal constraint of photosynthesis comprised the inhibition of g_s under reduced water content in plants and improved the effectiveness of water use (Yin *et al.* 2005). Similarly, as observed by Barbour *et al.* (2011), our experiment demonstrated that the WUE_i values were significantly lower in the control (PV2 and PV3) compared with the drought-treated seedlings with decreasing g_s and consequently increasing WUE_i. The values measured in PV2 and PV3 during the recovery might be slightly overestimated as we only measured the surviving seedlings, which were less affected by stress. The lowering of the soil water potential caused the stomata in young beech plants to close, and resulted in P_N at higher WUE_i (Goisser *et al.* 2013). This was also observed in the seedlings from PV1. Together with an almost unchanged P_N (6.2 µmol m^{-2} s^{-1}) in PV1 manifested the WUE_i that increased from 57.9 to 62.0 µmol(CO_2) mol^{-1}(H_2O), and the most significant lowering of ψ_{pd} values (–1.82 MPa). This finding allowed us to state that the seedlings from the PV1 were the most resistant against the treatment and stomatal constraints (Fig. 3). These observations corresponded with the results of RLCs during DS (Figs. 4*B*,*E*, 5*B*,*E*). The higher photosynthetic rate in PV1 might be an important quencher of excessive light energy. These quenching mechanisms were lacking in the seedlings from higher altitudes, and the PSII in these seedlings was not resistant to damage during extreme drought events. The results of RLCs indicated that the highest resistance to water deficit was recorded in the beech seedling of PV1, which originated in low-elevation localities in a relatively drier climate district. This confirms results of several studies that found a higher water deficit tolerance in provenances originating from the xeric eastern or southern distribution margin compared to those from the central part of the beech range (Czajkowski and Bolte 2006, Rose *et al.* 2009, Thiel *et al.* 2014).

Sanchéz-Goméz *et al.* (2013) determined that in beech seedlings from six examined provenances, the most vulnerable to water deficit were the seedlings originating in 880 m a.s.l. with a mean annual rainfall total of 1,316 mm. Sanchéz-Goméz *et al.* (2013) also observed that this provenance showed dramatically weaker restoration for several physiological variables (P_N, g_s, Φ_{PSII}) after rewatering when compared with other provenances. This observation is consistent with our findings concerning the seedlings from PV3 (1,250 m a.s.l., mean annual rainfall total of 1,096 mm). These seedlings were unable to restore their g_s (Fig. 3*B*) and Φ_{PSII} (Fig. 4*C*) to the original level after rewatering. A similar trend in g_s and Φ_{PSII} was observed in PV2. Beech seedlings exposed to water deficit for 36 d did not reach their original g_s values after the recovery period; the values of this variable after 2 d reached only 0.050 mol m^{-2} s^{-1} (Galle and Feller 2007).

Stomata play important role in water control (Galle and Feller 2007) and the decrease of g_s led to simultaneous decreases of ψ_{pd} and P_N. To test if water deficit could damage the PSII functionality, we coupled leaf gas-exchange measurements with measurements of Chl fluorescence (Maxwell and Johnson 2000).

In plants exposed to water deficit, the stomata normally close to prevent water loss, which results in a decrease in the intercellular CO_2 concentration and depression of photosynthesis (Mittal *et al.* 2011). Under these conditions, photoinhibition is induced in response to excessive amount of photons being absorbed *vs.* those being harvested in photosynthesis.

Adverse water conditions during water deficit reduced the rate of electron transport from PSII, which in turn negatively affected the q_P through a decrease in the activation of light-induced enzymes participating in carbon metabolism and the control of stomata opening (Maxwell and Johnson 2000). Even after the recovery period, the seedlings from PV2 and PV3 did not noticeably succeed in restoring their q_P values to the “normal” levels measured under the control conditions at the beginning of the experiment.

Nonphotochemical quenching increases exponentially with water loss (Zivcak *et al.* 2013), and it is enhanced under a heavy stress when P_N is reduced by half (Zivcak *et al.* 2013). Enhanced nonphotochemical quenching (q_N, NPQ) was observed in leaves, induced as their protective mechanisms (Maxwell and Johnson 2000). A tendency towards slightly higher NPQ values was detected in drought-stressed leaves in beech seedlings during the first 10 d of dehydration (Galle and Feller 2007). In our study, however, the same was observed only in seedlings from the PV1, and it was also observed during their recovery (Fig. 5*C*).

The parameters Φ_{PSII}, q_P, q_N, NPQ, and ETR unequivocally indicated provenance PV3 as the most vulnerable. The constrained water supply had also negative impacts on photosynthetic characteristics. We found that the PV3 (origin in 1,250 m a.s.l., humid climatic area) had the lowest resistance to water deficit and the lowest restoration capacity during the recovery.

We can conclude that progressive water deficit initialised an array of parallel changes affecting the physiological condition of the studied beech provenances. The intensity of these changes depended on the plant origin. The reduction of water available for seedlings (ψ_{pd} data) during water stress resulted in a significant decrease in the efficiency of primary photochemistry in PSII, most strongly in the provenance optimal for beech. However, the provenance originating in a humid climate (PV3) exhibited the lowest resistance to water deficit at the level of leaf gas exchange, as well as the poorest recovery ability after rewatering. The provenance originating in a drier climate (PV1) demonstrated the strongest resistance to drought stress. Due to evolutionary adaptation, a population includes only those drought-tolerant individuals who can inherit this adaptive capacity to the next generation (Hampe and Petit 2005). These facts also support our hypothesis that beech plants from provenances with more frequent drought periods are less sensitive to water deficit in the future. The information we provided on ecotypes thriving from lower drought sensitivity could be useful in the process of selection of drought-tolerant species and their provenances (Bolte *et al.* 2009).

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