

Light acclimation of European beech (*Fagus sylvatica* L.) saplings after canopy destruction

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Abstract

Gas exchange response of European beech (*Fagus sylvatica* L.) saplings to canopy opening was studied in the ‘Petrohan’ training and experimental forest range in Western Stara Planina Mt. Experimental plots were set on various altitudes (700–1450 m a.s.l.) and were chosen by their different silvicultural or disturbances histories. The results of this study point out that European beech saplings show significant acclimation potential to changed post-cutting or windthrow environmental conditions. The light response curves at saplings from the open and the closed sites were typical for the sun and the shade ecotype of European beech leaves. The maximal photosynthesis was higher in more illuminated saplings but, as with light-use efficiency, did not vary significantly with cutting type, disturbance, altitude and air temperature. These physiological indicators rather express the biological characteristics of the European beech more strongly than a common response to environmental changes. In contrast, respiration, transpiration, water-use efficiency and light-compensation points were highly correlated with altitude and temperature. Especially the respiration and the transpiration varied much less with cutting type and natural disturbance. The light-compensation point was the most sensitive to both the type of stand opening and illumination, which can indicate the acclimation response of European beech saplings to stand disturbances of different sizes and causes.

Key words: light-compensation point, light-use efficiency, photosynthesis, transpiration, water-use efficiency.

Introduction

European beech (*Fagus sylvatica* L.), a widely distributed European forest tree species, is at its south-eastern limit of distribution in the Bulgarian mountains between 600 and 1800 m elevation. Several factors, such as shade tolerance, manage species’ position in forest succession. Pi-

ioneer species are generally shade intolerant and rapidly grow in open ground. Late succession species survive under shading are somewhat intolerant to high light and grow slower (Leuschner and Ellenberg 2017).

Forest cuttings or disturbances can significantly alter the light environment experienced by forest saplings (Kozłowski

2002, Dietze and Clark 2008). The extent and nature of these changes depend on factors, such as the type and intensity of cuttings or disturbances, spatial distribution of canopy opening, as well as the surrounding forest structure. The type and distribution of forest cuttings can lead to spatial heterogeneity in light availability. Forest cuttings create edges between the cut area and the surrounding forest. The resulting edge effects can include increase in light penetration into the adjacent forest, creating transitional zones with higher light levels than the forest interior (Matlack and Litvaitis 1999, Zheng and Chen 2000).

The impact of forest cuttings on light availability may vary over time. Initially, there may be a period of intense light exposure following a cutting event, which gradually decreases as vegetation regrows and canopy closure occurs. Over time, the light environment may stabilize, but the composition and structure of the forest may still be altered compared to pre-cut conditions (Kermavnar et al. 2019). In selective logging or partial cutting scenarios, residual vegetation may remain in the stand, providing shade and modifying the light environment for saplings. Residual trees or shrubs can create a dappled light environment with varying shade and sun flecks, influencing sapling growth and regeneration (Wagner et al. 2011).

On the other hand, significant canopy destructions create a highly altered environment that can be critically stressful for saplings (Oliver 1980), especially late successional species, such as European beech. Large canopy openings and disturbances may expose beech saplings to increased environmental stresses, such as higher temperatures and more significant fluctuations in soil moisture. However, Dountchev and Zhelev (2015) found high

survivability after windthrow on the north-eastern slopes of Vitosha Mt., Bulgaria. They point out that beech and some pioneer species have a potential to restore windthrow areas effectively. In the large gaps, European beech is more adaptive, especially compared to high-sensitive to intense direct light species, e.g. silver fir. However, it does not realize such an advantage compared to spruce (Čater et al. 2014, Čater and Diaci 2017). Čater (2021) point out that the generally better adaptability of European beech after disturbances might be closely related to their annual foliage development, compared to conifers and the longevity of fir and spruce needles.

European beech retains its position after the windthrow due to the ample advance regeneration released by the disturbance (Szwagrzyk et al. 2018). European beech saplings can acclimate to canopy openings through physiological, morphological and growth-related responses (Lichtenthaler et al. 1981, 2007). These responses allow them to adjust to the changes in light availability, competition and other environmental factors associated with canopy openings (Thornley 2002). One of the most vital acclimation traits of the European beech to illumination change is its ability to develop leaves with different morphological characteristics – sun and shade ecotype leaves, which can enhance light capture and maximise photosynthetic rates in high-light environments (Wagner et al. 2010). Eschrich et al. (1989) point out that sun- and shade-leaf determination in European beech is triggered towards the end of July. When applied before July, changes in light conditions influence the structure of the next season's leaves. After the middle of August, an increase in irradiation has little or no influence on the structure of primordia

of the next season's leaves.

Sun and shade leaves grow in different light environments within a forest canopy (Niinemets 2010). These leaves exhibit several differences in photosynthetic characteristics to adapt to the varying light conditions. Sun leaves in beech typically have smaller surface areas but are thicker and with more packed chloroplasts than shade leaves (Closa et al. 2010). This acclimation allows sun leaves to maximise light absorption and photosynthetic efficiency in high-light environments. Shade leaves may have higher chlorophyll concentrations to optimise light capture and utilisation in low-light conditions (Closa et al. 2010, Anev et al. 2015).

Additionally, shade leaves may contain different ratios of chlorophyll a to chlorophyll b compared to sun leaves (Lichtenthaler et al. 2007). Sun leaves of European beech typically exhibit higher photosynthetic rates and maximal photosynthesis than shade leaves. This acclimation allows to capture and utilise the abundant light in high-light environments efficiently and maximise carbon assimilation. Shade leaves of European beech generally have lower photosynthetic rates and maximal photosynthesis due to the limited light availability in shaded environments (Lichtenthaler et al. 2013). However, shade leaves have a higher light-use efficiency in low-light conditions, in compare to sun leaves, due to their specialised morphology and light-harvesting capabilities (Lichtenthaler et al. 1981). European beech saplings successfully change their photosynthetic apparatuses to adapt to changes in light availability. This may include adjustments in chlorophyll content, chloroplast structure (Lichtenthaler et al. 1981, 2007), in the activity of photosynthetic enzymes (Kubiske and Pregitzer 1997) to optimize photosynthetic rates un-

der different light conditions.

According to Kaiser et al. (2015), studying the light response curve is essential to understand various factors that influence the photosynthetic efficiency of plants and how they respond to changes in their environment. The light response curve of photosynthesis represents the relationship between the photosynthesis rate and light intensity. According to Thornley (2002), at low light intensities, the rate of photosynthesis increases rapidly as light intensity increases. This phase occurs because the available light energy is insufficient to saturate the plant's photosynthetic apparatus and for this reason the rate of photosynthesis increases close to linearly with increasing light intensity. The second phase occurs when light intensity is at a level that saturates the photosynthetic capacity of the plant but does not cause damage to the photosynthetic apparatus. Beyond a certain light intensity, the rate of photosynthesis reaches a maximum level and plateaus. This occurs because the plant's photosynthetic apparatus becomes saturated with light energy, and the further increases in light intensity do not lead to a rise in the rate of photosynthesis and can even lead to photoinhibition (Wimalasekera 2019), although Wyka et al. (2007) did not establish a relationship between photoinhibition and shade tolerance in European beech. The shape of the light response curve may vary depending on factors, such as plant species, environmental conditions and the availability of other resources, such as carbon dioxide and water (Čater and Diaci 2017).

This study aimed to evaluate the potential of European beech saplings to acclimate the main physiological processes to changes in light regime and other microclimatic factors after different types of forest cutting and a large windthrow.

Materials and Methods

Experimental sites and plots

European beech (*Fagus sylvatica* L.) saplings' physiological responses to canopy opening were studied in the 'Petrohan' training and experimental forest range in Western Stara Planina Mt. The climate is mountainous with a moderate continental influence. The mean annual temperature at 1450 m is 4.8 °C, and the mean annual precipitation is about 1080 mm, with higher values in spring (Koleva and Peneva 1990, Kutchukova 1983). The soil is brown acid (district eutric cambisol) developed on granite, with a mean depth exceeding 80 cm (Malinova and Petrova 2019). Experimental sites were set on various altitudes (700–1450 m a.s.l.) in mono-dominated by European beech stands and were chosen according to their different silvicultural or disturbances histories. Each site includes two plots – stands with destructed and thus open (O) and closed (C) canopy stands for control (Table 1).

In 2011, the canopy of the ES1-O plot was opened by cutting off all mature trees (120 years) in a gap with sizes 25 × 40 m (0.1 ha), which was not subsequently expanded further. In 2013, the canopy (120-year-old) of the ES2-O plot opened a circle gap with a diameter of 50 m, which was expanded to 80 m (~0.5 ha) in 2018. In the winter of 2013/2014, the 80-year-old stand (ES3-O) was disturbed by a windthrow of a total area of ~2.5 ha. The canopy of ES4-O was opened by cutting off eight mature trees (160 years), evenly distributed on a total area of 0.1 ha. The control C-plots were placed near the O-plots in the stands, which have not been subject to logging or natural disturbance in at least the last twenty years.

The temperatures measured during the physiological measurements indicated that the areas with the canopy destruction were warmer. The differences vary from 0.39 °C on EP1 to 2.25 °C on EP3. Unlike the air temperature, the differences in relative humidity between the O and C plots were not unambiguous. The air was

Table 1. Characteristic of the open (O) and closed (C) canopy plots in experimental sites.

Experimental plot	Latitude, ° ' "	Longitude, ° ' "	Elevation, m	T_{AIR} , °C	HD, %	PPFD, $\mu\text{mol}(\gamma) \cdot \text{m}^{-2} \cdot \text{s}^{-1}$	<i>n</i>	<i>N</i>	N_L , $\text{mg} \cdot \text{g}_{dw}^{-1}$
ES1-C	43°7'32"	23°7'25"	1439	20.68 ± 0.07	56.6 ± 0.5	47.7 ± 5.8	22	176	17.3 ± 0.3
ES1-O	43°7'30"	23°7'23"	1450	21.07 ± 0.05	46.8 ± 0.2	912.7 ± 197.3	25	200	18.3 ± 0.4
ES2-C	43°8'22"	23°8'33"	970	22.72 ± 0.03	55.8 ± 0.2	39.0 ± 12.2	22	176	16.3 ± 0.2
ES2-O	43°8'23"	23°8'37"	1015	23.56 ± 0.10	56.5 ± 0.4	773.2 ± 244.2	25	200	17.0 ± 0.4
ES3-C	43°11'15"	23°7'32"	870	24.25 ± 0.11	59.2 ± 0.5	163.1 ± 95.2	20	160	17.2 ± 0.3
ES3-O	43°11'18"	23°7'33"	862	26.45 ± 0.14	46.3 ± 0.5	1125.5 ± 186.5	23	184	19.2 ± 0.7
ES4-C	43°9'29"	23°9'00"	713	25.11 ± 0.07	57.6 ± 0.3	171.5 ± 10.7	25	200	15.8 ± 0.2
ES4-O	43°9'27"	23°8'59"	718	26.22 ± 0.06	58.6 ± 0.4	385.2 ± 42.2	25	200	17.1 ± 0.3

Note: Average values ± standard error of air temperature (T , °C), relative air humidity (HD , %), and photosynthetic photon flux density (PPFD, $\mu\text{mol}(\gamma) \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) during the physiological measurements are presented. The number of light-response curves (n) and total number of measurements ($N = 8 \cdot n$) of each plot after data filtering are presented in the last two columns. N_L is the leaf nitrogen content ± SE.

drier in plots with a large disturbed canopy compared to the control plots – on ES1 with 9.8 % and ES3 with 12.9 %. However, the differences were insignificant at the ES with smaller canopy openings.

Total nitrogen concentration by Kjeldahl (Jones 1991) was determined on 100 leaves per plot in mixed sample from each O and C plot with three replications in 2019. The leaves of the lighted saplings tended to accumulate more nitrogen than those under the canopy, which was most pronounced in ES3 (windthrow).

Gas-exchange measurements

Gas exchange measurements were carried out in five consecutive growing seasons during the period 2018–2022 on typical, cloudless July days on five randomly chosen saplings with a similar height of around 1.5 m at each O and C plot. Net-photosynthetic rate (A_N) and transpiration rate (E) were measured on a third leaf of branches in the upper part of sapling's crown with a portable photosynthesis system Li-6400 (LiCor Instruments, Lincoln, NE, USA), equipped with shielded thermocouples, a red light-emitting diode light source (6400-02) and a quantum PAR sensor (LI-190) in the chamber. Before measurements, the instrument was calibrated according to standard procedures (LiCor 2012). Simultaneously with the physiological indicators, the air temperature (T_{AIR}), relative air humidity (HD) and photosynthetic photon flux density ($PPFD$) were recorded in the field measurements with the sensors built into the Li-6400. The summarized levels of these indicators are presented in Table 1.

Following the protocol of Evans and Santiago (2014), light-response curves for each leaf were recorded between 09:00–12:00 at ambient levels of envi-

ronmental factors: CO_2 -concentration at about $400 \mu\text{mol}(CO_2) \cdot \text{mol}^{-1}$, leaf temperature $20\text{--}26^\circ\text{C}$, $45\text{--}60\%$ relative humidity. Leaves were given at least 3 min. to acclimate to chamber conditions under a saturating irradiance of $1000 \mu\text{mol}(\gamma) \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ until TotalCV decreased below 0.5 %. Subsequently, the $PPFD$ was changed in incremental steps, using eight levels of illumination (2000, 1000, 500, 250, 100, 50, 25 and $0 \mu\text{mol}(\gamma) \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) changed by the auto program 'Light_curve', in which we set the following criteria: minimum acclimation time of the leaf when the $PPFD$ in the camera changes 60 s; maximum time before values are recorded 120 s; 'match mode' before each measurement; and TotalCV < 0.5 % (Broadbent 2012).

Photosynthetic light responses were individually analysed for each leaf with the non-rectangular hyperbolic model (Leverenz and Jarvis 1979, Marshall and Biscoe 1980, Prioul and Chartier 1977, Norman et al. 1992). Light-use efficiency (LUE , $\mu\text{mol}(CO_2) \cdot \mu\text{mol}(\gamma)^{-1}$), the maximal photosynthesis (A_{MAX} , $\mu\text{mol}(CO_2) \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), the dark respiration rate (R_D , $\mu\text{mol}(CO_2) \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) and the convexity (θ) of the light response curve were calculated for each sample. All regression lines were fitted to the data by applying the least-squares approach of the Microsoft Excel Solver routine using the Newton algorithm (Office 2019, Microsoft, Redmond, WA, USA). The light-compensation point (LCP , $\mu\text{mol}(\gamma) \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) was calculated by the regression equations as the $PPFD$, at which photosynthesis and respiration equalise ($A_N = 0$). Transpiration rates E , $\text{mmol}(H_2O) \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ of each leaf were calculated as the average value of transpiration, recorded at eight levels of $PPFD$ during the measurements for light curves. Water-use efficiency of each leaf was calculated as $WUE = A_N/E$,

$\mu\text{mol}(\text{CO}_2) \cdot \text{mmol}(\text{H}_2\text{O})^{-1}$.

Data were filtered before statistical processing according to the following criteria: $A_{\text{MAX}} > 0 > R_D$; $LCP > 0$; $0.125 > LUE > 0$; $E > 0$. One-way ANOVA tests and Tukey post hoc analysis were performed to determine the difference between the average values of A_{MAX} , R_D , LCP , LUE , E and WUE of saplings in O and C plots of experimental sites. All statistical procedures were performed with MS Excel and user-defined functions in Visual Basic for Applications (MS VBA 7.1, Microsoft, Redmond, WA, USA). Only statistically significant results (as defined by a P -value < 0.05) were discussed.

Results

Light-response curves

At all experimental sites, light curves of photosynthesis in the O-plots were typical for sun leaves and in C-plots they were typical for shade leaves (Fig. 1).

Photosynthesis saturates with light, reaches 90 % of its maximum at $PPFD$ between 250 and 500 $\mu\text{mol}(\gamma) \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ for the shade leaves (C-plots). At the same time, the sun leaves (O-plots) need significantly more intense light and their photosynthesis saturates above 1000 $\mu\text{mol}(\gamma) \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. The difference between the curves of the O and C plots is most significant at the highest altitude, while the curves converge at decreasing altitudes. Light curves of O and C plots in ES1 are crossed (A_N of O and C plots become equal) at 42 $\mu\text{mol}(\gamma) \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, in ES2 and ES4 – at 84 $\mu\text{mol}(\gamma) \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, and in ES3 – at 90 $\mu\text{mol}(\gamma) \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Only in few saplings from the C-plots we found lower photosynthesis at 2000 than at 1000 $\mu\text{mol}(\gamma) \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, which corresponds to the findings of Wyka et al. (2007). Li-

chtenthaler et al. (1981) point out that the acclimation of saplings to high quanta fluence rates is correlated with a higher photosynthetic capacity and especially with a higher light saturation of CO_2 -fixation. Čater and Diaci (2017) show that in beech, the acclimatization to light climate develops relatively faster than some evergreen species, which might be closely related to their annual foliage development compared to conifers and the longevity of fir and spruce needles (Čater 2021).

The maximal photosynthesis (A_{MAX}) is significantly higher in O-plots, than in C-plots, except for ES3, where the difference is minimal as there is measured the minimum A_{MAX} at illuminated saplings and the maximum A_{MAX} at shaded saplings among all sites (Fig. 2).

The A_{MAX} of illuminated saplings in ES1-O was 1.99 times higher than in ES1-C on a background of more than 19 times higher $PPFD$ in the gap. In ES2-O, $PPFD$ was 18.8 times higher than such in ES2-C, and yet the difference between A_{MAX} was 2.05 times in favour of the illuminated saplings. Differences in A_{MAX} between sun and shade leaves were similar to those previously described for European beech (Lichtenthaler et al. 1981, 2007). In the windthrow site (ES3-O), despite the highest average $PPFD$, compared to the other sites, it was only 6.9 times higher than the ES3-C and probably for this reason, an insignificant difference of A_{MAX} between ES3-O and ES3-C was observed. That may be due to the edge effects, which can increase light penetration into the nearby forest stands (Matlack and Litvaitis 1999, Zheng and Chen 2000). Čater (2021) establishes similar levels of A_{MAX} in European beech saplings in the second year after exposure to the rapid increase of light due to sleet damages to the mature canopy. He points out that the suc-

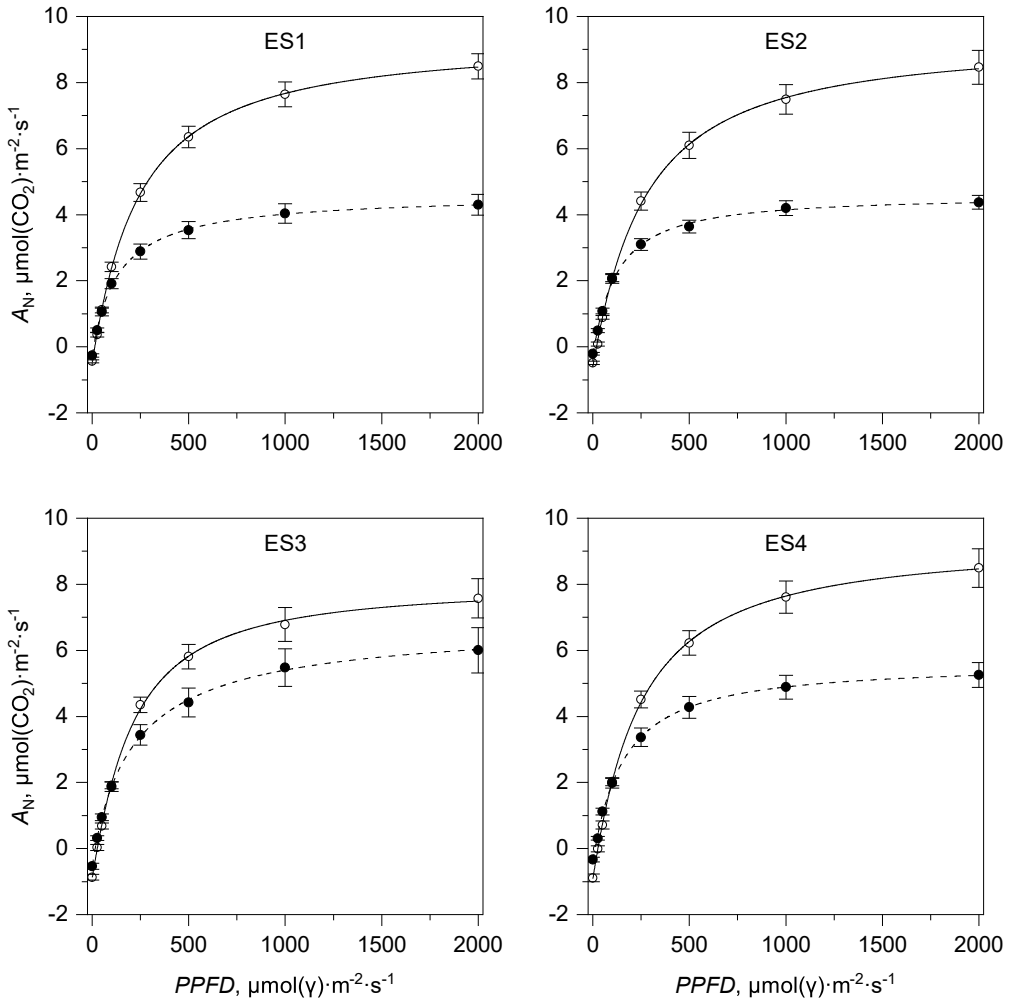


Fig. 1. Light-response curves of European beech saplings in the O-plots (—○—) and in the C-plots (- - ● - -) of experimental sites (ES1, ES2, ES3, and ES4).

Note: The mean values of net-photosynthetic rate (A_N) at various photosynthetic photon flux density ($PPFD$) are presented with circles. The standard errors of means are presented with whiskers. The lines presented regressions.

cessful acclimation of trees with advanced regeneration is mainly related to their ability to produce sun foliage. Reynolds and Frochot (2003) reported lag-missing in photosynthetic acclimation only four months after windthrow. This observation is similar to findings by Tognetti et al.

(1994) for well-watered, shade-acclimated beech seedlings, in which an increase in photosynthetic rates began even by the end of the first week after transfer to high illumination and was nearly complete after only one month.

Despite the higher $PPFD$ in the areas

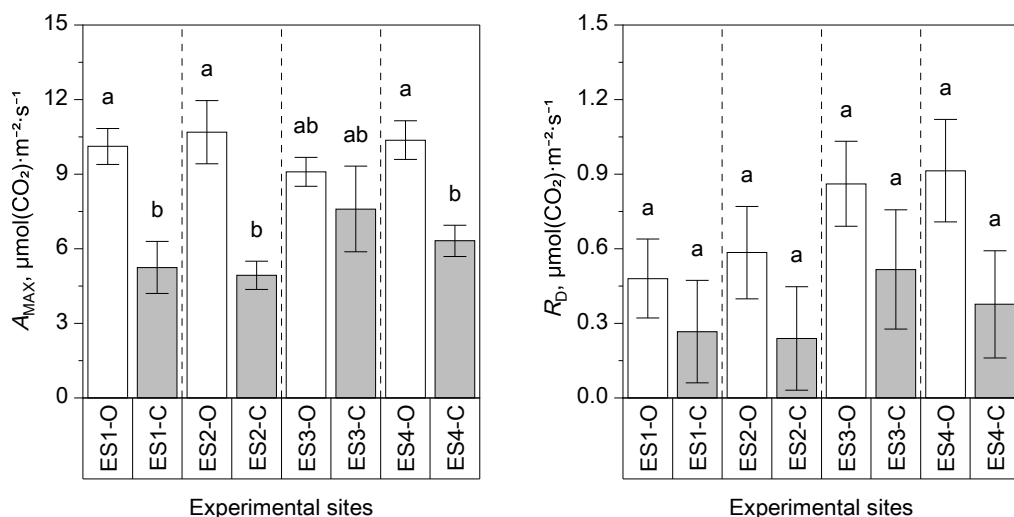


Fig. 2. Maximal photosynthesis (A_{MAX}) – left, and dark respiration rate (R_D) – right, of European beech saplings within saplings in the O-plots (□) and in the C-plots (■) of experimental sites (ES1, ES2, ES3, and ES4).

Note: The regression values (eq. 1) are presented with columns, and their standard errors are presented with whiskers. One-way ANOVA (Tukey) statistical test was applied to estimate the difference among all the variants. Different letters denote statistically significant differences.

with an open canopy, the air temperature was not appreciably affected (Table 1). This could explain the lack of significant differences between the R_D levels of the saplings in the open plots and under the assembly of the control areas. However, there was a strong negative correlation (Pearson correlation coefficient) between altitude and respiration rate ($R = -0.47$, $P\text{-value} < 0.001$) and a positive correlation between air temperature and respiration rate ($R = 0.48$, $P\text{-value} < 0.001$) of saplings in open canopy plots, already established by other authors (Hikosaka et al. 1999, Tjoelker et al. 2001, Smith and Dukes 2013).

The values of all the LCP of sun-acclimate saplings in O-plots were also significantly higher than the LCP of shade saplings in C-plots – 2.2 times on ES1, 2.43 times on ES2, 2.51 times on ES4 and only 1.71 times on windthrow (ES3) (Fig. 3).

As Lichtenthaler et al. (1981, 2007) and Kolev and Anev (2022) point out, lower chlorophyll concentration and more intense respiration in sun leaves result in a higher $PPFD$ to equalization photosynthesis and respiration. Like R_D , LCP in O-plots has a strong negative correlation (-0.340 , $P\text{-value} < 0.001$) with altitude and a strong positive correlation (0.345 , $P\text{-value} < 0.001$) with air temperature.

According to Čater (2021), quantum yield (or light-use efficiency) reflects the overall adaptation of the entire tree, especially in the upper third of the crown. He established that the LUE in European beech saplings increased in the years following the ice storm and windstorm. However, its studies have been carried out since the year after the destruction of the canopy, unlike ours, which occurs 5–7 years after cuttings or natural disturbance. In our experiment, LUE was not variate

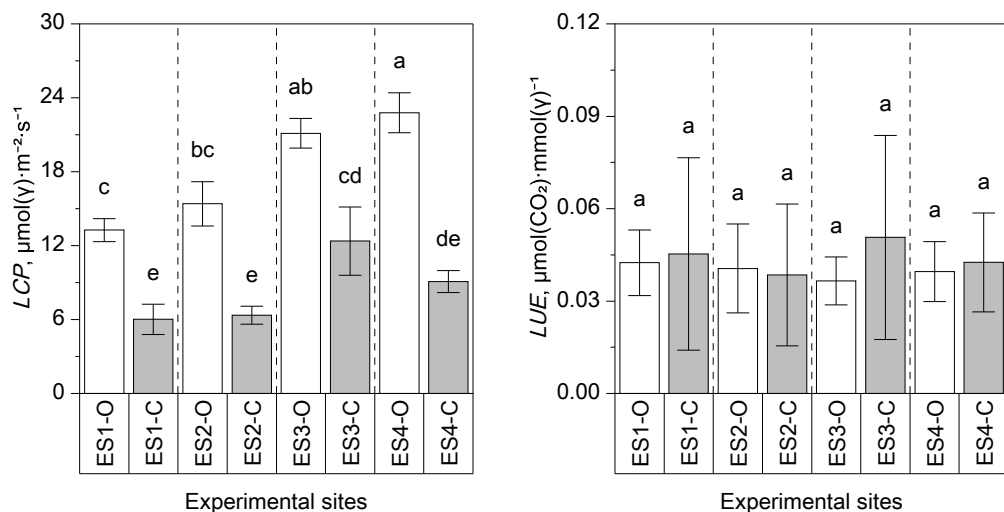


Fig. 3. Light-compensation point (*LCP*) – left, and light-use efficiency (*LUE*) – right, of European beech saplings in the O-plots (□) and in the C-plots (■) of experimental sites (ES1, ES2, ES3, and ES4).

Note: The regression values (eq. 1 and eq. 2) are presented with columns. The standard errors of regression values are presented with whiskers. One-way ANOVA (Tukey) statistical test was applied to estimate the difference among all the variants. Different letters denote statistically significant differences.

significant not only between the O-plots and the C-plots but also along the entire vertical profile of the experimental sites. This can be explained by, on one hand, the more minor scales of canopy destruction and, on the other hand, the more extended acclimatization period compared to similar experiments, e.g. Čater (2021).

The water regime of European beech saplings was much less affected than carbon assimilation. Both transpiration rates and *WUE* were not significantly different for saplings in O-plots and C-plots in all experimental sites (Fig. 4).

The results confirm our previous study (Anev and Marinova 2021), in which we hypothesized that the protective role of pioneer grass species allows European beech saplings to inhabit an environment with more humid air and maintain moderate levels of transpiration and *WUE*,

even after canopy disturbance. Reynolds and Frochot (2003) confirm that functional (physiological) changes in response to the new environment occurred sooner than structural (morphological) changes. However, as with respiration and *LCP*, transpiration, although less pronounced, had a significant negative correlation ($R = -0.29$, P -value < 0.001) with altitude and a significant positive correlation ($R = 0.30$, P -value < 0.001) with air temperature.

Conclusions

The results of this study indicate that European beech saplings show significant assimilation acclimation potential to change post-cutting or windthrow environmental conditions. The light curves are

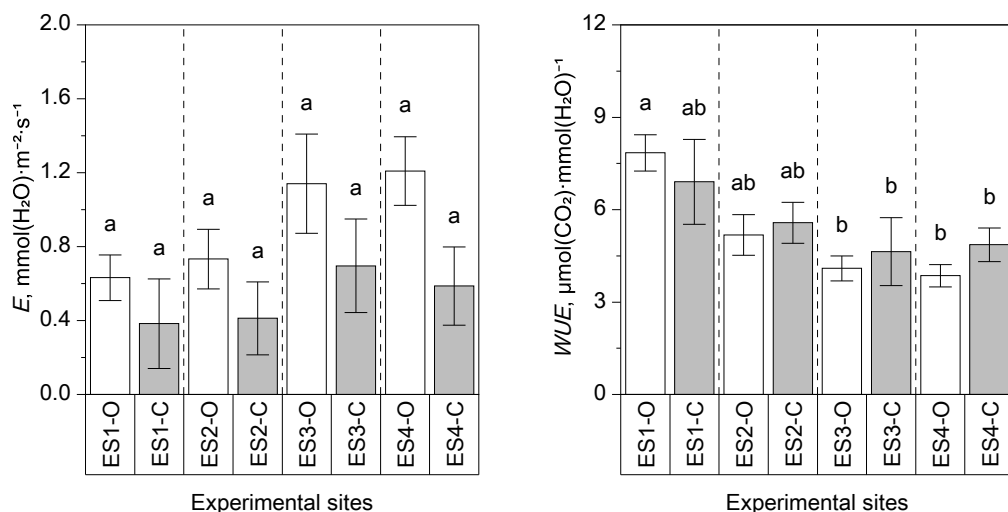


Fig. 4. Transpiration rate (E) – left, and water-use efficiency (WUE) – right, of European beech saplings in the O-plots (□) and in the C-plots (■) of experimental sites (ES1, ES2, ES3, and ES4).

Note: The mean values (eq. 3 and eq. 4) are presented with columns. The standard errors of mean values are presented with whiskers. One-way ANOVA (Tukey) statistical test was applied to estimate the difference among all the variants. Different letters denote statistically significant differences.

similar in all sites and visualize the typical change of photosynthesis with the change of illumination in the sun and in the shade ecotype of leaves. Maximal photosynthesis and light compensation points were higher in more illuminated plots. Dark respiration, light-use efficiency, transpiration rates and water-use efficiency did not vary significantly by cutting type or disturbance. We can conclude that these indicators reflect more strongly biological characteristics of the European beech typical sun and shade leaves than a response to environmental changes. Dark respiration, transpiration rate and light-compensation points were highly correlated with altitude and temperature. The light compensation point was the most sensitive to both the cause of stand opening and illumination, which can indicate the acclimation response of European beech saplings to

stand disturbances of different sizes and causes.

Acknowledgements

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