

Acclimation changes in photosynthesis of *Fagus sylvatica*, *Populus tremula*, and *Acer platanoides* after natural disturbance

Presented at the Conference 'A century of forest knowledge – education, innovations, challenges (CENFORKNOW 2025)', 7–9 May 2025, Sofia, Bulgaria

Thematic field: Climate change and forests

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Received: 23 May 2025 / Accepted: 04 August 2025 / Available online: 18 August 2025



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Abstract

Large-scale natural disturbances in forest ecosystems drastically alter the light regime for residual saplings within the affected areas, placing their survival under considerable threat. Light acclimation of photosynthesis represents a key physiological mechanism for maintaining a positive carbon balance, thereby enabling plants to preserve their protective functions within altered environments. The aim of this study was to assess interspecific differences in photosynthetic light acclimation and carbon-use efficiency in saplings of three forest tree species – *Fagus sylvatica* L., *Populus tremula* L. and *Acer platanoides* L. – following large-scale natural disturbances. These species were selected due to their contrasting ecological strategies: the shade-tolerant *F. sylvatica*, the light-demanding pioneer *P. tremula*, and the moderately plastic *A. platanoides*. A comparative analysis of parameters, such as A_{MAX} , R_D , LCP, and LSP reveals pronounced species-specific responses, reflecting divergent functional–ecological strategies. These findings provide deeper understanding of the mechanisms underpinning light acclimation and offer valuable insights for adaptive forest management, particularly considering the increasing frequency and intensity of climate-induced disturbances. The results may support improved predictions of regeneration dynamics and species resilience under future forest conditions.

Key words: carbon balance, light-response curve, photosynthetic plasticity.

Introduction

Temperate forest ecosystems have been facing significant challenges arising from the intensifying impacts of climate change. In recent decades, there has

been a marked increase in the frequency and severity of natural disturbances, such as windthrows, wildfires, and droughts, which have led to abrupt alterations to microclimatic conditions within affected areas, including the light regime, particularly

in the understorey layer (Seidl et al. 2017). Such disturbances result in the removal of substantial portions of the forest canopy, allowing intense light to penetrate to the regenerating saplings below. The sudden change in light availability for these young trees represents both a potential threat and an opportunity for growth, provided they possess effective mechanisms for acclimation.

Light acclimation of photosynthesis plays a pivotal role in enabling plants to sustain a positive carbon balance, which is critical not only for growth but also for the activation of metabolic pathways associated with defence and recovery following stress (Valladares and Niinemets 2008). Plants exhibit species-specific strategies in response to light stress, ranging from rapid physiological adjustments to structural modifications in leaf morphology and photosynthetic apparatus (Niinemets and Valladares 2006).

Fagus sylvatica L., as a shade-tolerant species, demonstrates limited plasticity, yet its capacity to maintain stable photosynthetic activity under low irradiance confers it with a competitive advantage in dense, closed-canopy forests. A study by Marinova and Anev (2024) has confirmed that small canopy openings created through carefully planned group selection cutting provide more favourable conditions for the growth of young beech saplings than large canopy destruction. Under such conditions, these individuals are able to develop more successfully without experiencing severe physiological stress or loss of leaf area, indicating that light, moisture, and temperature remain within tolerable ranges that the plant can effectively utilise. In other words, moderate canopy thinning facilitates beech regeneration without exposing the saplings to excessive ecological risk. Additionally, Anev (2024) reports

that following canopy removal, *F. sylvatica* responds physiologically by increasing the light compensation point, in its quest to adjust to increased light availability. These findings demonstrate that, despite its reputation as a shade-tolerant species, beech possesses considerable capacity for light acclimation under specific silvicultural or naturally disturbed conditions.

Populus tremula L. exhibits exceptionally high photosynthetic plasticity, allowing rapid adaptation to newly illuminated environments following canopy openings (Wittmann et al. 2001, Vodde et al. 2010). Such a strategy frequently results in the dominance of the species during the early successional stages following disturbance (Valladares and Niinemets 2008). *Acer platanoides* L. occupies an intermediate position between shade-tolerant and light-demanding species (San-Miguel-Ayanz et al. 2016). Although it favours partial shade, it demonstrates a moderate adaptive capacity to increased irradiance. This is achieved through both structural (Kloeppel and Abrams 1995) and functional leaf-level modifications, including variations in the content of photosynthetic pigments (Gitelson et al. 2009) and the photochemical activity of photosystem II (Lichtenthaler et al. 2013). These responses are consistent with the findings of Ciupak et al. (2019), who highlight the high seasonal plasticity of leaf physiology in this species.

The importance of light acclimation becomes even more pronounced in the context of climate change, where elevated temperatures, irregular precipitation, and the growing occurrence of extreme weather events increasingly constrain forest regeneration processes (Anderegg et al. 2020). Thus, the frequency of disturbances and the capacity of individual species to establish and persist in disturbed areas become critical to the future resilience of

forest ecosystems (Seidl et al. 2017). Investigating light acclimation in young individuals of *F. sylvatica*, *P. tremula*, and *A. platanoides* yields valuable insights into species-specific resilience and regeneration potential (Vodde et al. 2010). A detailed understanding of interspecific differences in light acclimation is essential for modelling forest dynamics and designing adaptive forest management strategies in the face of a changing climate (Brodribb et al. 2020).

The aim of this study was to assess interspecific differences in photosynthetic light acclimation and carbon-use efficiency in saplings of *Fagus sylvatica*, *Populus tremula*, and *Acer platanoides* following large-scale natural disturbances.

Materials and Methods

Objects and plant material

The gas exchange responses of European beech (*F. sylvatica* L.), Eurasian aspen (*P. tremula* L.), and Norway maple (*A. platanoides* L.) saplings to changes in light conditions following canopy disturbance were examined in the Petrohan training and experimental forest range, located in the Western Balkan Mountains. The selection of species was based on their contrasting ecological strategies: *F. sylvatica* as a shade-tolerant species adapted to low light availability; *P. tremula* as a pioneer, light-demanding species with high physiological plasticity; and *A. platanoides* as an intermediate strategist (San-Miguel-Ayanz et al. 2016). This design facilitated the assessment of interspecific differences in photosynthetic acclimation in response to disturbances of varying intensity and ecological impact.

The climate of the region is mountainous with moderate continental influence.

At an elevation of 1450 m, the mean annual temperature is 4.8 °C, while the average annual precipitation reaches approximately 1080 mm, with markedly higher values in spring (Kutchukova 1983, Koleva and Peneva 1990). According to Marinova and Bocheva (2023), the average temperature anomaly in Bulgaria for the reference period 1991–2020, compared to 1961–1990, was 0.8 °C. Unlike the average annual air temperature, no significant change in the annual precipitation amount was detected during this period. Marinova and Bocheva (2023) reported that temperature anomalies in the Western Balkan Mountains region ranged between 0.5 °C in autumn and 1.5 °C in summer. At the same time, precipitation rates have decreased by an average of 10–20 mm per year, particularly in winter and spring.

All three tree species were represented by naturally regenerated saplings growing in the same plots. The first sample plot (SP-14) was situated at an altitude of 876.1 m, 25.3° sloped in N-NE direction, and had been disturbed by windthrow in January 2014, ten years before measurements (Fig. 1).

The second sample plot (SP-21) was established in an area disturbed in 2021 by an ice storm, at an altitude of 946.8 m and with a 10.8° slope in the NE direction. A control plot (SP-0) was located between the two experimental plots. SP-0 lay within a closed-canopy forest, mono-dominated by *F. sylvatica*, approximately one-hundred-year old, at an altitude of 888.6 m with a 13.3° slope facing north, and had not been affected by disturbances in 2014 and 2021.

Gas-exchange measurements

Gas-exchange measurements were carried out under clear and cloudless skies on typical June days in 2024. For each

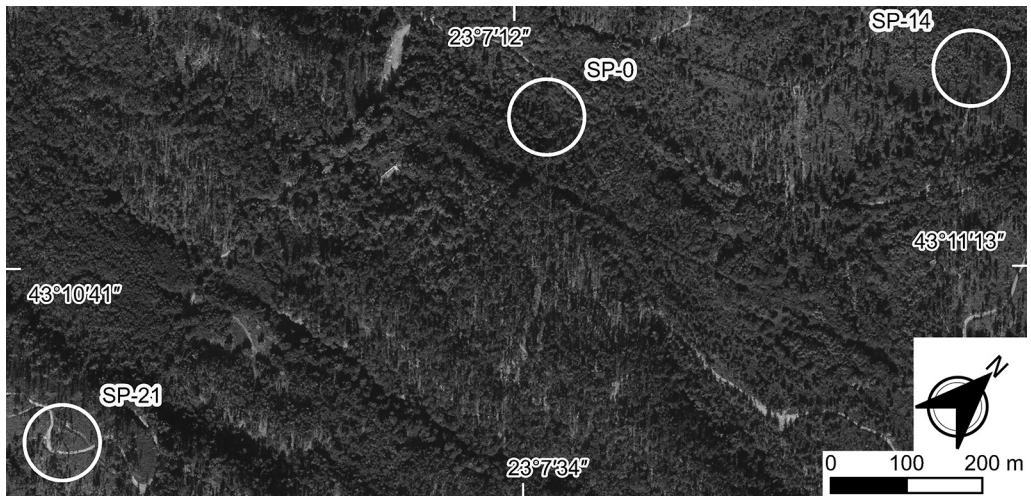


Fig. 1. Aerial view of studied region with sample plots (Inspire 2023).

measurement, five saplings per species (*F. sylvatica*, *P. tremula*, *A. platanoides*) were randomly selected on each plot. Net photosynthesis rate (A_N) was measured on the third fully expanded leaf, located on a branch from the middle section of the crown, using a Li-6800 portable photosynthesis system (LI-COR Biosciences, Lincoln, NE, USA) with Firmware v.2.1.11. The 3×3 cm leaf chamber (6800-12A; LI-COR) equipped with blue-red LEDs (6800-02; LI-COR) and a quantum PAR sensor (Li-190) was used. Prior to each measurement series, the instrument was calibrated according to the manufacturer's standard procedures (Li-Cor 2022). Each leaf underwent at least 3 min of acclimation at saturating irradiance ($1000 \mu\text{mol}(\gamma) \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) until stable readings with a total coefficient of variation (TotalCV) below 0.5 % were achieved. The auto-programme 'Light Curve' was used to measure net photosynthesis at eight levels of photosynthetic photon flux density (PPFD), following a survey strategy (Li-Cor 2022). The 'Light curve' settings were light values: 2000, 1000, 500,

250, 100, 50, 25, 0; min wait: 60 s; max wait: 120 s; check early match. Before the measurements, the chamber environment was stabilised with a flow of $500 \mu\text{mol} \cdot \text{s}^{-1}$; fan speed 10,000 rpm; ambient and stable CO_2 (around 400 ppm), H_2O (around 50 %), and air temperature (around 25°C).

Photosynthetic light-response curves were analysed separately for each leaf by fitting a non-rectangular hyperbolic model (Thornley 1976, Prioul and Chartier 1977, Leverenz and Jarvis 1979, Marshall and Biscoe 1980, Norman et al. 1992). The following parameters were calculated: light-use efficiency ($\text{LUE}, \mu\text{mol}(\text{CO}_2) \cdot \mu\text{mol}(\gamma)^{-1}$), maximum photosynthetic rate ($A_{\text{MAX}}, \mu\text{mol}(\text{CO}_2) \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), dark respiration rate ($R_D, \mu\text{mol}(\text{CO}_2) \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), and the convexity (θ) of the light-response curve. All regression curves were fitted using the least-squares method via the Newton algorithm in Microsoft Excel (Office 365, Microsoft, Redmond, WA, USA), using VBA script (Visual Basic for Application, v.7.1.1146, Microsoft, Redmond, WA, USA). The light compensation point ($\text{LCP}, \mu\text{mol}(\gamma) \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)

was derived from the regression equations as the PPFD value, at which the rate of net photosynthesis equals zero ($A_N = 0$). One-way ANOVA tests and Fisher's LSD test were performed to assess the difference between the average values of A_{MAX} , R_D , LCP, LSP, LUE, and CUE of experimental sites. The carbon-use efficiency (CUE) was calculated as the ratio of the maximum photosynthetic rate (A_{MAX}) and the dark respiration rate (R_D), i.e. $CUE = A_{MAX} \cdot R_D^{-1}$. This approach reflects an approximation of the balance between carbon gain and respiratory carbon loss at the leaf level and has been adapted from the methodology proposed by Anev and Damyanova (2024) and Marinova and Anev (2023). It conceptually parallels the definition of CUE at the whole-plant and ecosystem scale, where CUE is commonly expressed as the ratio of net to gross primary production (NPP/GPP), as initially formulated by Thornley and Cannell (2000). Although alternative formulations exist – such as $CUE = (A_{MAX} - R_D) \cdot A_{MAX}^{-1}$ – these expressions are mathematically interrelated and provide equivalent biological interpretations within the physiological context of leaf gas exchange.

Results and Discussion

Analysis of the photosynthetic light-response curves indicated that the lowest rates of photosynthetic activity were consistently recorded beneath the forest canopy in all three investigated species (Fig. 2).

Following natural disturbances, *P. tremula* demonstrated rapid and pronounced acclimation. Saplings exhibited photosynthetic rates approximately 1.6 times higher than those observed beneath the canopy, achieving the highest A_{MAX} among the three species (Fig. 3).

This corresponds with the observations of Wittmann et al. (2001), who reported that *P. tremula* possesses high photosynthetic plasticity and shows rapid induction under fluctuating light conditions. Additionally, Roden and Pearcy (1993) noted that leaves of *Populus* species maintain high photosynthetic efficiency under variable light environments, highlighting their capacity for rapid adaptation to dynamic light regimes.

Nevertheless, the elevated rates of dark respiration (R_D), particularly in 2021, when they were twice those recorded be-

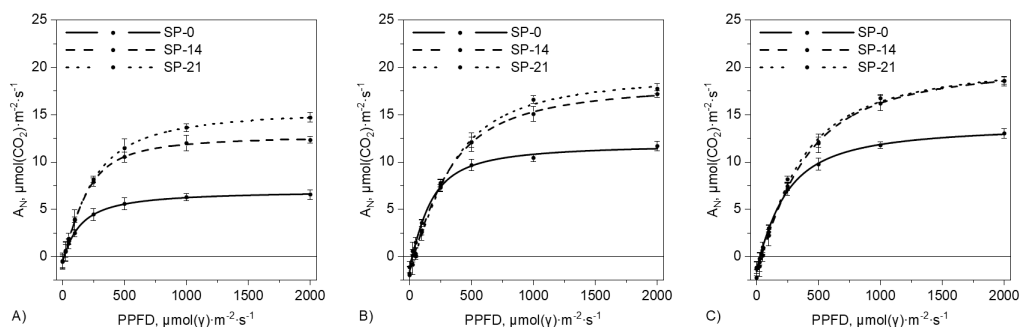


Fig. 2. Light curves of photosynthesis in A) *F. sylvatica*, B) *A. platanooides*, C) *P. tremula* saplings under the canopy (SP-0), in disturbed 2014 (SP-14), and disturbed 2021 (SP-21) sample plots.

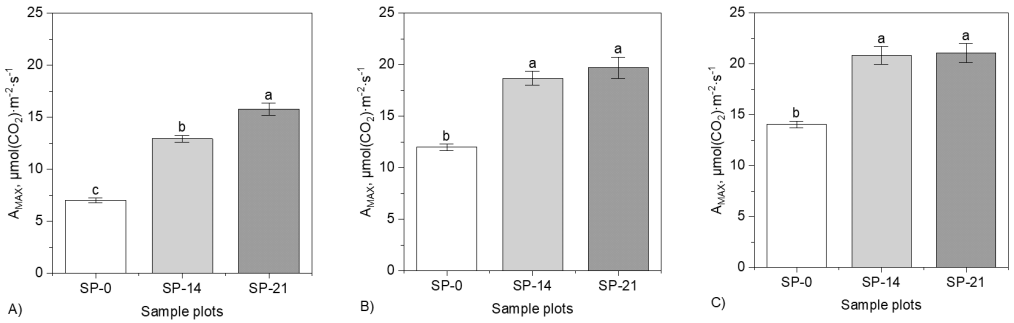


Fig. 3. Maximal photosynthesis in A) *F. sylvatica*, B) *A. platanoides*, C) *P. tremula* saplings under the canopy (SP-0), in disturbed 2014 (SP-14), and disturbed 2021 (SP-21) sample plots.

Note: The data are presented as mean $\pm$ SE. Means that do not share a letter are significantly different (One-way ANOVA with Fisher's LSD test, P -value < 0.05).

neath the canopy and 4.8 times greater than those recorded for *F. sylvatica*, indicate substantial carbon costs that may constrain the net carbon balance of the species (Fig. 4).

Furthermore, a study by Dai et al. (2021) has shown that elevated ozone levels can impair the thermal acclimation of photosynthesis in *P. tremula*, highlighting the species' vulnerability to combined stress factors, such as pollution and increased temperatures. *A. platanoides* also displayed substantial acclimation fol-

lowing disturbance, with increased values of A_{MAX} and LSP (figs 2 and 5).

Nevertheless, R_D in this species (Fig. 4) peaked in 2021, which may be attributed to elevated temperatures and drought conditions. A study by Carón et al. (2015) demonstrated that this species is highly sensitive to the combined effects of increased temperature and reduced soil moisture, resulting in diminished seedling survival and growth. These findings highlight the limited plasticity of *A. platanoides* under extreme climatic conditions.

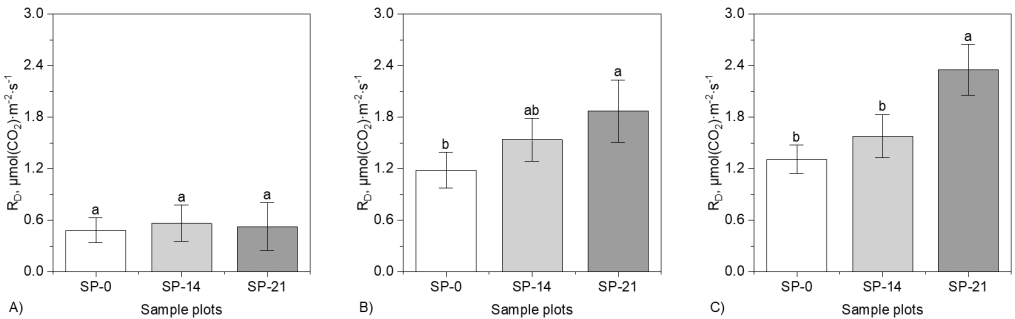


Fig. 4. Dark respiration in A) *F. sylvatica*, B) *A. platanoides*, C) *P. tremula* saplings under the canopy (SP-0), in disturbed 2014 (SP-14), and disturbed 2021 (SP-21) sample plots.

Note: The data are presented as mean $\pm$ SE. Means that do not share a letter are significantly different (One-way ANOVA with Fisher's LSD test, P -value < 0.05).

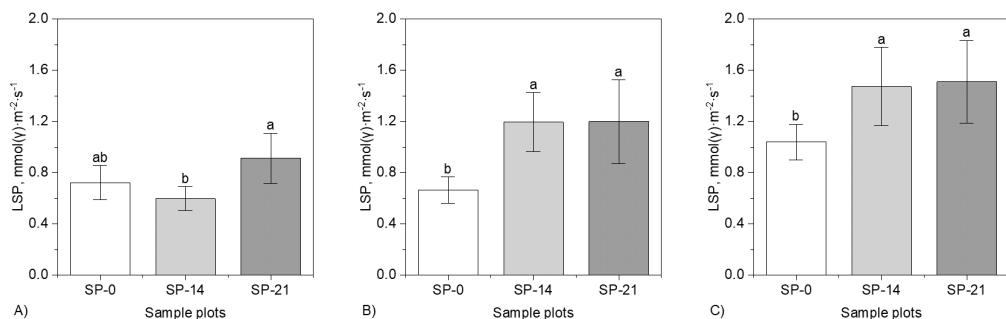


Fig. 5. Light-saturation points in A) *F. sylvatica*, B) *A. platanoides*, C) *P. tremula* saplings under the canopy (SP-0), in disturbed 2014 (SP-14), and disturbed 2021 (SP-21) sample plots.

Note: The data are presented as mean $\pm$ SE. Means that do not share a letter are significantly different (One-way ANOVA with Fisher's LSD test, P -value < 0.05).

A recent study by Urban et al. (2023) revealed that *A. platanoides* responds to drought by enhancing photoprotective mechanisms, specifically through an increase in non-photochemical energy dissipation (Φ_{NPQ}), which serves to mitigate the damaging effects of reactive oxygen species. However, even following the cessation of drought conditions, the species maintains elevated Φ_{NPQ} levels, suggesting a long-term physiological adaptation that may, nonetheless, result in reduced photosynthetic efficiency under chronic stress. These results confirm the species' moderate tolerance to water deficit and underscore the importance of carefully managing light and moisture regimes in regeneration contexts.

Moreover, research by Banks (2018) emphasises that *A. platanoides* exhibits distinct fluorescence characteristics under drought conditions, which may serve as indicators for assessing the physiological status of plants. This further supports the significance of *A. platanoides* as a competitively capable species under diverse environmental conditions, particularly in the context of ongoing climate change.

F. sylvatica, known for its shade tol-

erance, displayed a marked increase in photosynthetic activity in saplings exposed to open conditions following disturbance, reaching values up to 1.6 times higher than those recorded under dense forest shade. This enhancement was accompanied by low and stable rates of dark respiration (R_D), contributing to the highest CUE among the three studied species (Fig. 6).

Similar findings were reported by Kraj and Ślepaczuk (2022), who observed that under increased irradiance, beech leaves adapt through structural modifications and increased leaf area, while maintaining photosynthetic efficiency and antioxidant defence. These results underscore the ability of *F. sylvatica* to successfully adjust to varying light regimes without compromising physiological stability. Anev and Marinova (2021) further demonstrated that, despite an initial decline in photosynthetic activity following windthrow events, saplings of this species recovered water-use efficiency and chlorophyll content within few years, indicating long-term physiological adaptation to altered light conditions.

Morphological plasticity, including var-

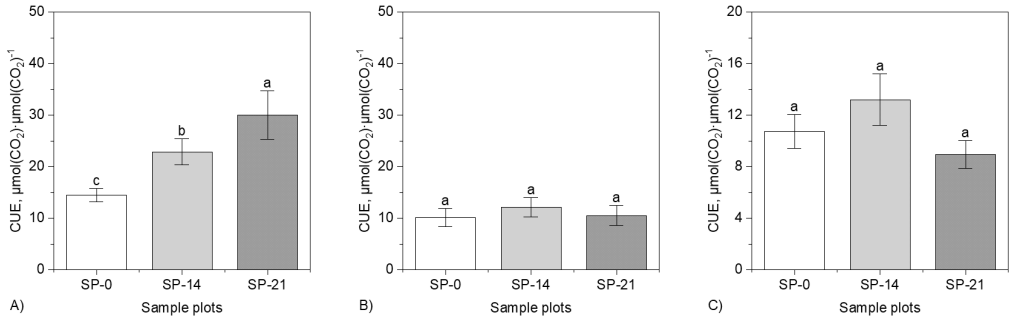


Fig. 6. Carbon-use efficiency in A) *F. sylvatica*, B) *A. platanoides*, C) *P. tremula* saplings under the canopy (SP-0), in disturbed 2014 (SP-14), and disturbed 2021 (SP-21) sample plots.

Note: The data are presented as mean $\pm$ SE. Means that do not share a letter are significantly different (One-way ANOVA with Fisher's LSD test, P -value < 0.05).

iation in leaf area, also contributes to the acclimation potential of beech saplings under changing environmental conditions. Anev et al. (2016) demonstrated that leaf area in *F. sylvatica* can be reliably estimated using a non-destructive model based on linear dimensions, which reflects underlying structural adjustments to light availability. These adaptations, when combined with physiological responses, support the species' capacity to maintain carbon balance and optimise light capture in heterogeneous environments.

This capacity for resilience is not limited to abiotic factors. *F. sylvatica* has also exhibited biochemical defence responses under biotic stress. Lamom et al. (2016) reported that herbivory by *Orchestes fagi* induced significant oxidative stress in beech leaves, particularly at lower altitudes, as reflected in elevated malondialdehyde (MDA) and proline levels. These findings highlight the species' ability to initiate antioxidative mechanisms while sustaining physiological performance. In addition, Anev and Damyanova (2024) found that *F. sylvatica* maintains stable light- and carbon-use efficiency throughout the growing season, even under seasonal fluctuations

in light intensity, confirming the species high plasticity.

Recently, a study by Provazník et al. (2024) investigated the photosynthetic performance of *F. sylvatica* saplings originating from different altitudes and geographical regions and planted in Denmark. The results indicated that saplings from higher elevations exhibited superior photosynthetic efficiency and adaptation to the new conditions, underscoring the importance of provenance in determining the species' adaptive potential. These findings reinforce the status of *F. sylvatica* as a species with high physiological resilience and adaptability to changing environmental conditions.

A comparative analysis of light compensation points (LCP), *F. sylvatica* had the lowest values, consistent with its shade-tolerant nature and capacity for efficient photosynthesis under low light availability. In contrast, *P. tremula* and *A. platanoides* showed higher LCP values, particularly in saplings examined in 2014 and 2021, suggesting greater light requirements to sustain a positive carbon balance (figs 7 and 8).

These findings are supported by re-

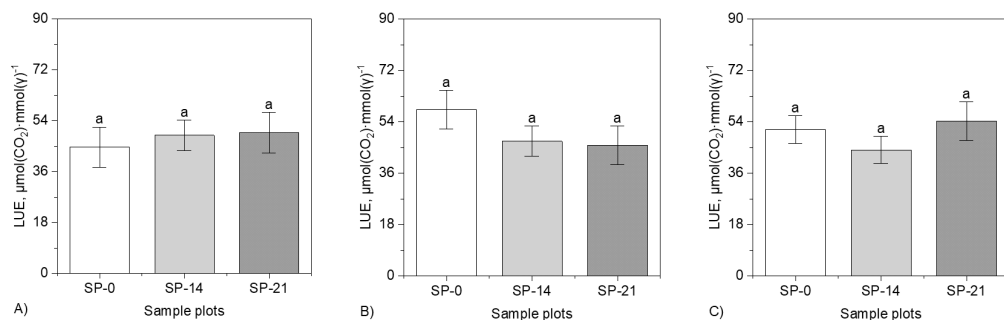


Fig. 7. Light use efficiency of photosynthesis in A) *F. sylvatica*, B) *A. platanoides*, C) *P. tremula* saplings under the canopy (SP-0), in disturbed 2014 (SP-14), and disturbed 2021 (SP-21) sample plots.

Note: The data are presented as mean $\pm$ SE. Means that do not share a letter are significantly different (One-way ANOVA with Fisher's LSD test, P -value < 0.05).

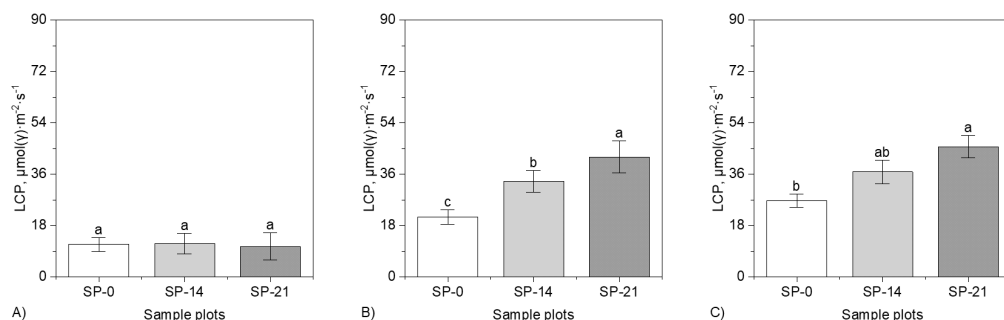


Fig. 8. Light compensation points in A) *F. sylvatica*, B) *A. platanoides*, C) *P. tremula* saplings under the canopy (SP-0), in disturbed 2014 (SP-14), and disturbed 2021 (SP-21) sample plots.

Note: The data are presented as mean $\pm$ SE. Means that do not share a letter are significantly different (One-way ANOVA with Fisher's LSD test, P -value < 0.05).

search conducted by Pfanz et al. (2002), which demonstrated that *F. sylvatica* possesses exceptionally low LCP and high light-use efficiency, rendering it highly competitive in shaded habitats. Conversely, a study by Kloeppel and Abrams (1995) reported that *A. platanoides* exhibits higher LCP values and lower photosynthetic efficiency under low light conditions, thereby limiting its capacity for growth in shaded environments.

In summary, the results clearly illustrate substantial interspecific differences

in both the extent and nature of light acclimation and carbon-use efficiency among saplings of *P. tremula*, *A. platanoides*, and *F. sylvatica* following natural disturbances to the forest canopy. *P. tremula* exhibits exceptionally rapid photosynthetic adaptation to altered conditions; however, this is accompanied by elevated dark respiration rates, which may potentially offset the benefits of accelerated carbon flux. *A. platanoides* displays a moderate photosynthetic response and a degree of resilience, yet remains sensitive to wa-

ter deficit and thermal stress, which may compromise its long-term competitive potential. In contrast, *F. sylvatica*, traditionally classified as a shade-tolerant species, demonstrates high physiological stability, characterised by low respiratory losses and high carbon-use efficiency, underscoring its capacity to maintain productivity under limited light availability. These species-specific differences are crucial for understanding their respective roles in forest regeneration processes and for predicting the structural dynamics of mixed forests in the context of increasing ecological disturbances.

Conclusions

The present study emphasises the pivotal role of photosynthetic plasticity in the acclimation of tree species to changing environmental conditions. The findings demonstrate that *P. tremula* and *A. platanoides* exhibit a high degree of light acclimation, as evidenced by increased values of maximum photosynthesis (A_{MAX}) and light saturation point (LSP) following natural disturbances. Nevertheless, *F. sylvatica* displayed the highest CUE, attributed to its low dark respiration rates, which underscores its physiological resilience and adaptability to shaded environments. Natural disturbances substantially affect the photosynthetic activity of young trees, leading to marked alterations in key physiological parameters, such as A_{MAX} , LSP, R_d , and LCP. These changes are strongly species-specific and highlight the need for a differentiated approach to evaluating regeneration potential and promoting sustainable forest development under changing climatic conditions. Understanding interspecific differences in adaptation mechanisms is essential for optimising sil-

vicultural strategies, including regeneration management, habitat restoration, and the conservation of forest ecosystems. In this context, the integration of physiological indicators into models of future forest development may enhance the effectiveness of adaptive management in the face of increasing ecological uncertainty.

Acknowledgements

The collection and processing of this data were carried out as part of implementing NIS-B-1292/2023 project at the University of Forestry, Bulgaria. The measurements were technically supported by infrastructure LTER-BG (Agreement No TO1-320/30.11.2023), purchased under the National Roadmap for Scientific Infrastructure and financially co-ordinated by the Ministry of Education and Science of Bulgaria.

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