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Seasonal variations of gas exchange parameters in mono-dominated by *Fagus sylvatica* and *Picea abies* stands

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Abstract

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In carrying out the long-term ecological monitoring activities in the forest site “Petrohan”, the seasonal variations of photosynthetic light-response curves were studied in mono-dominated by European beech (*Fagus sylvatica* L.) natural forest and Norway spruce (*Picea abies* Karst.) plantation in West Stara Planina Mountain. The results showed that light curves vary much more during vegetation season in Norway spruce than in European beech. While the beech had gas-exchange parameters confirming its shade tolerance, the spruce was more intolerant to shade. Maximal photosynthesis was highest in spruce in June and permanently decreased in August and October. In contrast to spruce, beech did not have a clear vegetative peak in gas exchange. Still, it achieved a stable carbon balance and a higher carbon-use efficiency, especially before the middle of the growing season. The light-use efficiency of beech and spruce remained relatively constant at whole studied season, confirming this parameter’s species-specific character.

Keywords: light-response curve; seasonal variation; LTER forest site

Introduction

Long-Term Ecological Research (LTER), is a network of research sites that study ecological processes for prolonged periods. The main goal of LTER is to improve understanding of ecosystems and their changes over time, including the impacts of climate change and human activities. LTER can provide insights into complex ecological dynamics by focusing on long-term data collection, allowing researchers to observe extended trends, cycles, and ecosystem changes. Such observations are critical for understanding climate change, species interactions, and ecosystem health (Callahan, 1984). A core value of LTER is the open sharing of data with the broader scientific community. Therefore, LTER plays a vital role in understanding ecosystems’ long-term dynamics, helping inform environmental policy, conservation efforts, and sustainable management practices worldwide (Robertson et al., 2012).

The LTER program started in the United States in 1980, but now has counterparts globally (Callahan, 1984). LTER-Bulgaria was founded in 2007 and has been a member of the LTER network since 2009. Site “Petrohan” is a substantial forest site within the national network for long-term research and the European Ecological Network LTER, thanks to its extensive, systematic collection of biometric, chemical, and physiological data over the years (Anev et al., 2023). The forests are mainly composed of natural European beech (*Fagus sylvatica* L.) stands, but in the mid-20th century, forest plantations were created from Norway spruce (*Picea abies* Karst.). Both natural European beech forests and artificially created plantations of Norway spruce are subject to escalating climate change. The challenges facing forests composed of late-successional species, such as European beech and Norway spruce, are mostly related to the need to acclimatize long-lived trees to the rapid pace of environmental change.

One of the first acclimatization changes in plants is related to the gas exchange of the leaves, especially to their carbon and water balance (Lambers & Oliveira, 2019; Schulze et al., 2019). 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 first phase occurs, because the available light energy is insufficient to saturate the plant's photosynthetic apparatus, and therefore, 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. Such saturation occurs because the light-independent phase of photosynthesis is much slower than light-dependent, and cannot absorb a high amount of ATP and NADP(H) produced under intense light (Farazdaghi, 2011), which can even lead to photo inhibition (Giovagnetti & Ruban, 2015; Wimalasekera, 2019). However, Wyka et al. (2007) did not establish a relationship between photoinhibition and shade tolerance, e.g. in European beech. Even more, the shape of the light response curve may vary depending on factors, such as internal factors for plants (Köstner et al., 2002), or environmental conditions, e.g., the availability of resources, such as carbon dioxide, temperature (Darenova et al., 2024), and water (Granier et al., 2007). Against this background, the light response curve of photosynthesis can be used in a wide range of ecological experiments to study acclimation to the dynamics of complex environmental factors (Leverenz, 1988; Reynolds & Frochot, 2003) and as a base for calculating forest net-primary productivity (Gao et al., 2023; Jarvis & Leverenz, 1983; Johnson & Thornley, 1984).

Most studies based on the light response curve of photosynthesis have been conducted once per growing season (Gardiner et al., 2009; Marinova & Anev, 2023; Shahanova et al., 2018); some are performed in the regime of a vegetation experiment (Tognetti et al., 1997; Tognetti et al., 1994), and others are carried out in the laboratory (Ben et al., 1987; Todorova et al., 2022; Todorova et al., 2023), which may skew or distort the results (Naumburg & Ellsworth, 2002). Few experiments are conducted in the field, following the vegetation dynamics of light dependence parameters of photosynthesis (Anev, 2024; Čater & Levanič, 2013). Such a design could provide valuable information on the efficiency of crucial environmental resources and, therefore, on the acclimatization potential of populations. The experiment's main objective was to trace the vegetation dynamics of resource use efficiency, such as light, carbon, and water of European beech and Norway spruce forests, in their natural conditions at the LTER forest site "Petrohan".

Material and Methods

Objects

Forest site "Petrohan" is located in the University of Forestry's training and experimental forest range, spanning 7,190.5 hectares in the West Stara Planina Mountain. The forests are mainly composed of natural European beech (*Fagus sylvatica* L.) stands, but in the mid-20th century, forest plantations were created from Norway spruce (*Picea abies* Karst.). The physiological measurements were carried out in two permanent sample plots – one mono-dominated by European beech and the other by Norway spruce. Two plots were situated at a small physical distance and similar altitude, a prerequisite for similar environmental conditions (Table 1).

Table 1. Description of sample plots

	Beech plot	Spruce plot
Altitude, m	1447	1413
Latitude, °	43.121	43.120
Longitude, °	23.121	23.128
Slope, °	21.24	10.65
Aspect, °	143 (SE)	272 (W)
Main tree species	*Fagus sylvatica* L.	*Picea abies* Karst.
Tree height, m	28	30
Diameter of breast height, cm	34	34
Age, years	140	90
Canopy closure, %	80–85	60–75

Methods

Gas exchange measurements were performed on five randomly selected trees between 10:00 and 13:00 on typical, cloudless days in June, August, and October 2023. The net photosynthetic rate was measured in various lights using the Portable Photosynthetic System Li-6800 (LI-COR Bioscience, Lincoln, NE, USA), equipped with a blue-red diode light source in the chamber. During the measurements, the Photosynthetic Photon Flux Density (PPFD) with 90% red and 10% blue light in the chamber was decreased in incremental steps, using eight levels (2000, 1000, 500, 250, 100, 50, 25, and 0 $\mu mol_{\gamma} \cdot m^{-2} \cdot s^{-1}$) changed by the automatic program, in which we set the following criteria: minimum acclimation time of the leaf, when the PPFD in the camera changed 60 s; a maximum time before values were recorded 120 s; “match mode” before each measurement (Li-Cor, 2022). Photosynthetic light responses were individually analyzed for each tree with the non-rectangular hyperbolic model (Prioul & Chartier, 1977). 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, USA). Light-use efficiency (LUE), the maximal photosynthesis (A_{MAX}), and the dark respiration rate (R_D) were calculated by the regressions. The light-compensation point (LCP) and light-saturation point (LSP) were calculated as the PPFD, at which photosynthesis and respiration equalize ($A_N = 0$) and photosynthesis reached 80% of A_{max}, respectively. Carbon-use efficiency (CUE) was calculated as a ratio between A_{MAX} and R_D. All mean values ($n = 5$) were compared by One-way ANOVA and Fisher’s post-hoc analysis ($P\text{-value} < 0.05$) (Zar, 2014).

Results and Discussion

Light curves vary much more **during vegetation season** in Norway spruce than in European beech. In June, the still young needles of spruce are not saturated with light even at the maximum daily illumination, in August, their light curve becomes similar to that of beech, while in October, photoinhibition is observed at illumination higher than 1000 $\mu mol_{\gamma} \cdot m^{-2} \cdot s^{-1}$ (Fig. 1).

Although Stinziano et al. (2015) suggests prolonged net carbon uptake by Norway spruce as a consequence of increased autumn temperatures, our observed results show that after dry summers, such as that in 2023, spruce photosynthesis is depleted in autumn. Similar substantial hysteresis in the light response curve in spruce forests was observed by Krupková et al. (2019). Our October results correspond to those established by Wyka et al. (2007), who found greater photoinhibition in Norway spruce than in European beech when both are adapted to full sunlight. The significantly more stable nature of beech light response curves may be result of the fact this species is native to the region and has evolved under the local climate. However, against the background of rapid climate change, stable light response curves can be taken as a positive signal of a preserved acclimatization potential of this species in Western Stara Planina Mountain. According Krupková et al. (2019), spruce reacts by closing its stomata before noon and maintaining a reduced photosynthetic activity for the rest of the day, while beech keeps its stomata open as long as possible and slightly reduces photosynthetic activity evenly throughout the entire day.

Maximal photosynthesis was highest in spruce in June, and permanently decreased about 1.84 times in August, and 3.64 times in October. At the same time, in beech, it was about 1.75 times lower at the beginning of the growing season, but did not change significantly during the following months (Fig. 2 A). The expense element of leaf carbon balance respiration was more intense in spruce at most months of vegetation. The maximal difference was realized in August, when spruce respired 2.82 times more intensively than beech, in June, this difference was almost half (1.45 times), while in October, the two species respire with similar intensity (Fig. 2 B).

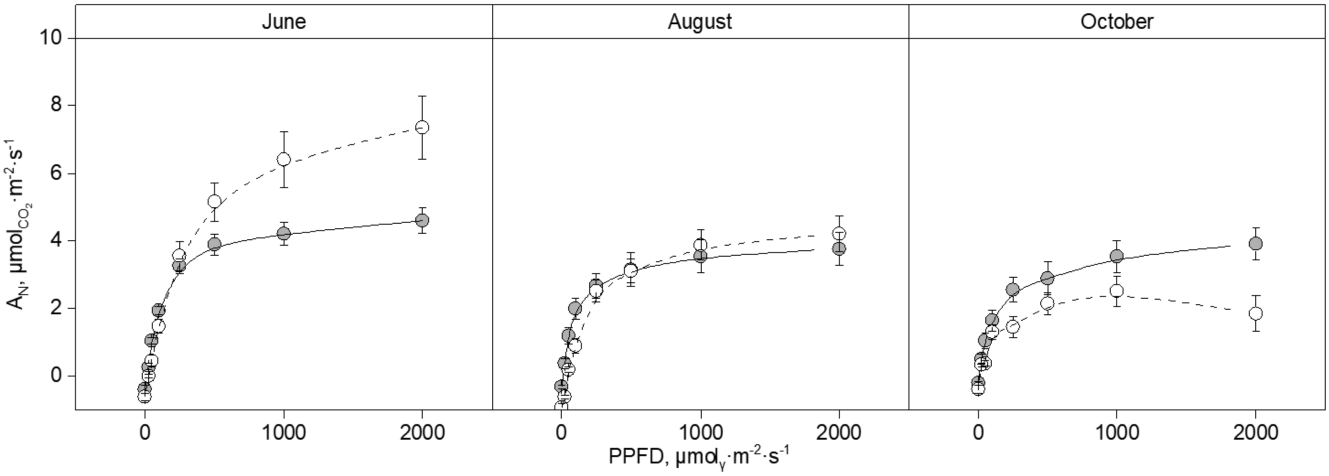

Fig. 1. Light response curves of European beech (grey dots, connected with solid line) and Norway spruce (white dots, coupled with dashed line) during June, August, and October 2023. The data are presented as mean ± SE (n = 5)

The cost of shade tolerance in a more closed canopy beech plot may involve reduced photosynthetic capacity in June, decreased respiration in all months, and, thus, vulnerability to photoinhibition damage in October. At the same time, spruce starts the growing season with a much higher photosynthetic capacity, but consumes a significant proportion of the assimilates produced, leading to impaired carbon use efficiency, which is probably the cause of the exhaustion in October (Fig. 2 C). However, Schulze et al. (1977) point out that the annual CO_2 uptake by evergreen spruce was higher than that of deciduous beech, not because of a long growing season or higher photosynthesis, but because of the longevity of its needles. During their total lifetime (an average of 5 years), evergreen spruce needles have a two to three times greater CO_2 uptake than a deciduous leaf in one summer season.

The light compensation point (LCP), strongly influenced by respiration, was also significantly higher in spruce than in beech throughout the period studied except in October. This difference varied from 1.97 times in June to 5.15 times in

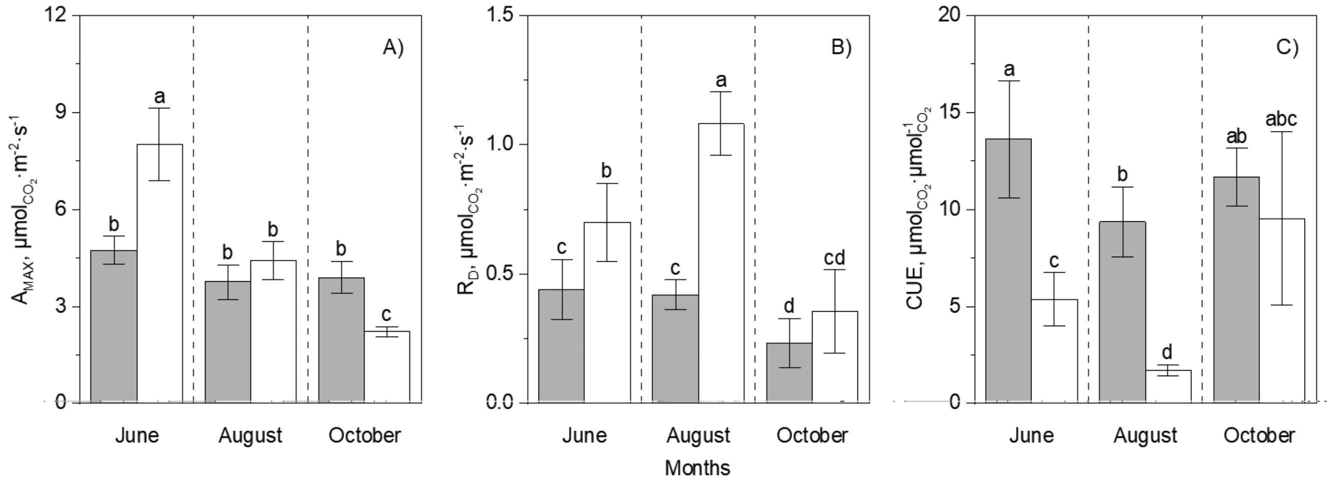

Fig. 2. Light-curves parameters A) maximal photosynthesis (A_{MAX}); B) dark respiration rate (R_D); C) carbon-use efficiency (CUE) in European beech (grey bars) and Norway spruce (white bars). The data are presented as mean ± SE (n = 5). Means that do not share a letter are significantly different (One-way ANOVA with Fisher's LSD test, P-value < 0.05)

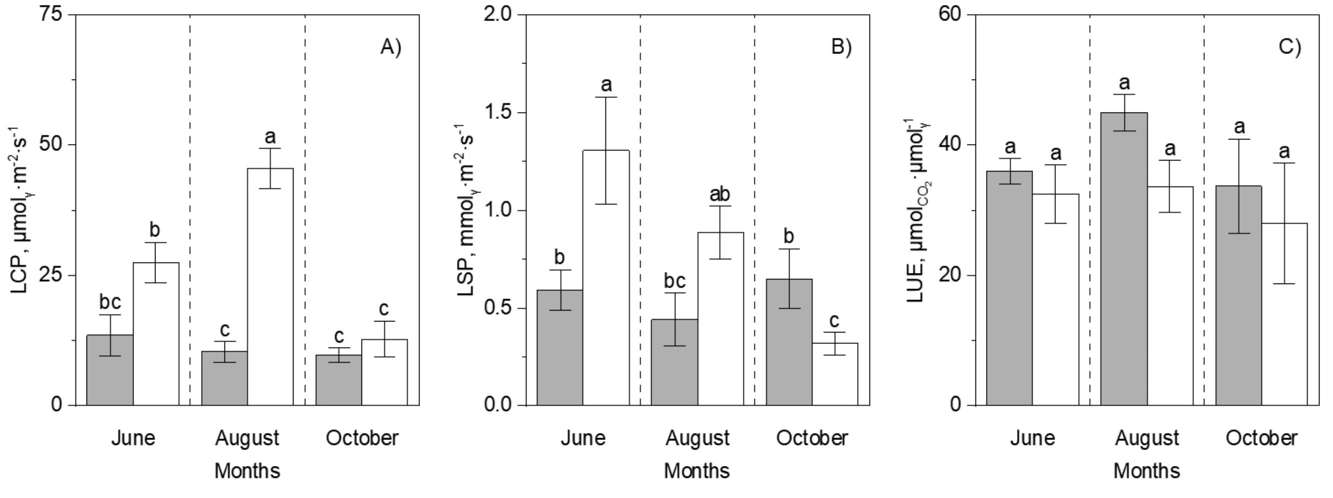

Fig. 3. Light-curves parameters A) light-compensation point (LCP); B) light-saturation point (LSP); C) Light-use efficiency (LUE) in European beech (grey bars) and Norway spruce (white bars). The data are presented as mean ± SE (n = 5). Means that do not share a letter are significantly different (One-way ANOVA with Fisher's LSD test, P-value < 0.05)

August (Fig. 3 A). At the same time, saturating light (LSP), which was more strongly influenced by maximum photosynthesis, was significantly higher in spruce in June (2.57 times) and in August (1.69 times), but in October, the trend was reversed when beech needs more intensive light (2.04 times) to saturate its photosynthesis (Fig. 3 B).

However, results in the same region show that European beech saplings can adequately respond to incident light, increasing LCP, while maintaining stable light-, carbon-, and water-use efficiency (Anev, 2024). Leuchner et al. (2011) point out that more PAR can penetrate the canopy at a lower zenith angle (e.g., in June), which is more pronounced for spruce than for beech. This is due to the conical crown shape of the conifers, which allows photons from higher angles to enter the gaps between trees in contrast to the more homogeneously closed beech canopy. Combined with the lower canopy closer in the spruce plot, this may explain the June light response curve's character and parameters typical of a shade-intolerant species. While the light-use efficiency of beech and spruce remains relatively constant, it is insignificant lower in spruce than that of beech throughout the entire vegetation period (Fig. 3 C).

Conclusions

Although often indicated as species with similar ecological niches, European beech and Norway spruce significantly differ in environmental resource use efficiency. While the beech has gas-exchange parameters that confirm its shade tolerance, the spruce is more intolerant to shade species. Spruce realizes its maximum photosynthetic activity in June as a gymnosperm species that starts the vegetation later and has a tenser water regime due to its primitive xylem. Still, its costs are most significant in August when temperatures are also the highest. In contrast, beech does not have a clear vegetative peak in gas exchange but achieves a higher carbon-use efficiency, especially before the middle of the growing season.

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Conflict of interest

The authors have no conflicts of interest to declare.

References

Anev, S. (2024). Light acclimation of European beech (*Fagus sylvatica* L.) saplings after canopy destruction. *Foresry Ideas*, *30*(1), 66-78. https://forestry-ideas.info/issues/issues_Download.php?download=504.

Anev, S., Tonchev, T., Dimitrova, V. & Damyanova, S. (2023). Methodological approach for long-term ecological research in forest sites. *Ecologia Balkanica*, *15*(2), 148-155.

Ben, G.-Y., Osmond, C. B. & Sharkey, T. D. (1987). Comparisons of Photosynthetic Responses of Xanthium strumarium and Helianthus annuus to Chronic and Acute Water Stress in Sun and Shade. *Plant Physiology*, *84*(2), 476–482. https://doi.org/10.1104/pp.84.2.476.

Callahan, J. T. (1984). Long-Term Ecological Research. *BioScience*, *34*(6), 363-367. https://doi.org/10.2307/1309727.

Čater, M. & Levanič, T. (2013). Response of Fagus sylvatica L. and Abies alba Mill. in different silvicultural systems of the high Dinaric karst. *Forest Ecology and Management*, *289*, 278-288. https://doi.org/10.1016/j.foreco.2012.10.021.

Darenova, E., Adamič, P. C. & Čater, M. (2024). Effect of temperature, water availability, and soil properties on soil CO_2 efflux in beech-fir forests along the Carpathian Mts. *CATENA*, *240*, 107974. https://doi.org/10.1016/j.catena.2024.107974.

Farazdaghi, H. (2011). The single-process biochemical reaction of Rubisco: A unified theory and model with the effects of irradiance, CO_2 and rate-limiting step on the kinetics of C3 and C4 photosynthesis from gas exchange. *BioSystems*, *103*(2), 265–284. https://doi.org/10.1016/j.biosystems.2010.11.004.

Gao, G., Hao, Y., Feng, Q., Guo, X., Shi, J. & Wu, B. (2023). Estimating canopy stomatal conductance and photosynthesis in apple trees by upscaling parameters from the leaf scale to the canopy scale in Jinzhong Basin on Loess Plateau. *Plant Physiology and Biochemistry*, *202*, 107939. https://doi.org/10.1016/j.plaphy.2023.107939.

Gardiner, E. S., Löf, M., O'Brien, J. J., Stanturf, J. A. & Madsen, P. (2009). Photosynthetic characteristics of *Fagus sylvatica* and *Quercus robur* established for stand conversion from *Picea abies*. *Forest Ecology and Management*, *258*(5), 868–878. https://doi.org/10.1016/j.foreco.2009.03.022.

Giovagnetti, V. & Ruban, A. V. (2015). Discerning the effects of photoinhibition and photoprotection on the rate of oxygen evolution in Arabidopsis leaves. *Journal of Photochemistry and Photobiology B: Biology*, *152*, 272-278. https://doi.org/10.1016/j.jphotobiol.2015.09.010.

Granier, A., Reichstein, M., Bréda, N., Janssens, I. A., Falge, E., Ciais, P., Grünwald, T., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Facini, O., Grassi, G., Heinesch, B., Ilvesniemi, H., Keronen, P., Knohl, A., Köstner, B., Lagergren, F.,…Wang, Q. (2007). Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agricultural and Forest Meteorology*, *143*(1-2), 123–145. https://doi.org/10.1016/j.agrformet.2006.12.004.

Jarvis, P. G. & Leverenz, J. W. (1983). Productivity of temperate, deciduous and evergreen forests. In *Physiological Plant Ecol-*

ogy IV (pp. 233–280). Springer. https://doi.org/10.1007/978-3-642-68156-1_9.

Johnson, I. R. & Thornley, J. H. M. (1984). A model of instantaneous and daily canopy photosynthesis. *Journal of Theoretical Biology*, *107*(4), 531–545. https://doi.org/10.1016/S0022-5193(84)80131-9.

Kaiser, E., Morales, A., Harbinson, J., Kromdijk, J., Heuvelink, E. & Marcelis, L. F. M. (2015). Dynamic photosynthesis in different environmental conditions. *Journal of Experimental Botany*, *66*(9), 2415-2426. https://doi.org/10.1093/jxb/eru406.

Köstner, B., Falge, E. & Tenhunen, J. D. (2002). Age-related effects on leaf area/sapwood area relationships, canopy transpiration and carbon gain of Norway spruce stands (Picea abies) in the Fichtelgebirge, Germany. *Tree Physiology*, *22*(8), 567–574. https://doi.org/10.1093/treephys/22.8.567.

Krupková, L., Havránková, K., Krejza, J., Sedlák, P. & Marek, M. V. (2019). Impact of water scarcity on spruce and beech forests. *Journal of Forestry Research*, *30*(3), 899-909. https://doi.org/10.1007/s11676-018-0642-5.

Lambers, H. & Oliveira, R. S. (2019). *Plant Physiological Ecology* (3 ed.). Springer. https://doi.org/10.1007/978-3-030-29639-1.

Leuchner, M., Hertel, C. & Menzel, A. (2011). Spatial variability of photosynthetically active radiation in European beech and Norway spruce. *Agricultural and Forest Meteorology*, *151*(9), 1226-1232. https://doi.org/10.1016/j.agrformet.2011.04.014.

Leverenz, J. W. (1988). The effects of illumination sequence, CO_2 concentration, temperature and acclimation on the convexity of the photosynthetic light response curve. *Physiologia Plantarum*, *74*(2), 332–341. https://doi.org/10.1111/j.1399-3054.1988.tb00639.x.

Li-Cor. (2022). *Using the LI-6800 Portable Photosynthesis System* (2 ed.).

Marinova, A., & Anev, S. (2023). Gas-exchange responses to light variation of tree species in urban landscaping. *Foresry Ideas*, *29*(2), 287-299. https://forestry-ideas.info/issues/issues_Download.php?download=494.

Naumburg, E. & Ellsworth, D. S. (2002). Short-term light and leaf photosynthetic dynamics affect estimates of daily understory photosynthesis in four tree species. *Tree Physiology*, *22*(6), 393–401. https://doi.org/10.1093/treephys/22.6.393.

Prioul, J. L. & Chartier, P. (1977). Partitioning of Transfer and Carboxylation Components of Intracellular Resistance to Photosynthetic CO_2 Fixation: A Critical Analysis of the Methods Used. *Annals of Botany*, *41*(4), 789–800. http://aob.oxfordjournals.org/content/41/4/789.abstract.

Reynolds, P. & Frochot, H. (2003). Photosynthetic acclimation of beech seedlings to full sunlight following a major windstorm event in France. *Annals of Forest Science*, *60*(7), 701–709. https://doi.org/10.1051/forest:2003064.

Robertson, G. P., Collins, S. L., Foster, D. R., Brokaw, N., Ducklow, H. W., Gragson, T. L., Gries, C., Hamilton, S. K., McGuire, A. D., Moore, J. C., Stanley, E. H., Waide, R. B. & Williams, M. W. (2012). Long-Term Ecological Research in a human-dominated World. *BioScience*, *62*(4), 342-353. https://doi.org/10.1525/bio.2012.62.4.6.

Schulze, E.-D., Beck, E., Buchmann, N., Clemens, S., Müller-Hohenstein, K. & Scherer-Lorenzen, M. (2019). *Plant Ecology*. Springer. https://doi.org/10.1007/978-3-662-56233-8.

Schulze, E. D., Fuchs, M. & Fuchs, M. I. (1977). Spacial distribution of photosynthetic capacity and performance in a mountain spruce forest of Northern Germany. *Oecologia*, *30*(3), 239-248. https://doi.org/10.1007/BF01833630.

Shahanova, M., Anev, S. & Tzvetkova, N. (2018). Gas exchange parameters for ornamental species of the genus Peperomia Ruitz et Pav., grown in a vertical garden under different nutrient conditions. *2nd International Conference on Sustainability, Human Geography and Environment*, Sopot, Poland.

Stinziano, J. R., Hüner, N. P. A. & Way, D. A. (2015). Warming delays autumn declines in photosynthetic capacity in a boreal conifer, Norway spruce (Picea abies). *Tree Physiology*, *35*(12), 1303-1313. https://doi.org/10.1093/treephys/tpv118.

Thornley, J. H. M. (2002). Instantaneous canopy photosynthesis: analytical expressions for sun and shade leaves based on exponential light decay down the canopy and an acclimated non-rectangular hyperbola for leaf photosynthesis. *Annals of Botany*, *89*(4), 451–458. https://doi.org/10.1093/aob/mcf071.

Todorova, D., Aleksandrov, V., Anev, S. & Sergiev, I. (2022). Photosynthesis Alterations in Wheat Plants Induced by Herbicide, Soil Drought or Flooding. *Agronomy*, *12*(2). https://doi.org/10.3390/agronomy12020390.

Todorova, D., Aleksandrov, V., Anev, S. & Sergiev, I. (2023). Comparative Study of Photosynthesis Performance of Herbicide-Treated Young Triticale Plants during Drought and Waterlogging Stress [Article]. *Agronomy-Basel*, *13*(8), 14. https://doi.org/10.3390/agronomy13081992.

Tognetti, R., Johnson, J. D. & Michelozzi, M. (1997). Ecophysiological responses of *Fagus sylvatica* seedlings to changing light conditions. I. Interactions between photosynthetic acclimation and photoinhibition during simulated canopy gap formation. *Physiologia Plantarum*, *101*(1), 115–123. https://doi.org/10.1111/j.1399-3054.1997.tb01827.x.

Tognetti, R., Michelozzi, M. & Borghetti, M. (1994). Response to light of shade-grown beech seedlings subjected to different watering regimes. *Tree Physiology*, *14*(7-8-9), 751-758. https://doi.org/10.1093/treephys/14.7-8-9.751.

Wimalasekera, R. (2019). Effect of Light Intensity on Photosynthesis. In: *Photosynthesis, Productivity and Environmental Stress*, 65-73. https://doi.org/10.1002/9781119501800.ch4.

Wyka, T., Robakowski, P. & Zytkowiak, R. (2007). Acclimation of leaves to contrasting irradiance in juvenile trees differing in shade tolerance. *Tree Physiology*, *27*(9), 1293-1306. https://doi.org/10.1093/treephys/27.9.1293.

Zar, J. H. (2014). *Biostatistical analysis*. Pearson Education Limited. http://books.google.bg/books?id=LCRFAQAAIAAJ.

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