FORESTRY IDEAS, 2023, vol. 29, No 2 (66): 287–299

Gas-exchange responses to light variation of tree species in urban landscaping

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Received: 04 October 2023 / Accepted: 13 November 2023 / Available online: 17 November 2023

Abstract

Some modifications of the urban environment, such as changes in light intensity resulting from anthropogenic activities in the cities, affect the plant's physiology. Examining physiological processes reveals the current state of plants and their potential for adaptation under changing environmental conditions. In a field study, we investigated the gas-exchange responses of seven tree species used in urban landscaping (*Betula pendula* Roth, *Ailanthus altissima* Swingle, *Tilia tomentosa* Moench, *Tilia platyphyllos* Scop., *Tilia cordata* Mill., *Quercus robur* L., and *Paulownia tomentosa* Siebold & Zucc) to variations of light using infrared gas analysis. Leaf light-saturated photosynthesis, dark respiration, and light use efficiency were obtained from the light-response curves. Carbon use efficiency was also determined. In this study, the highly shade-intolerant species, except for *P. tomentosa*, show lower carbon use efficiency. This suggests that the existing environmental conditions are not conducive to intensive growth for species that demand substantial solar radiation. In contrast, *P. tomentosa* stands out as an exceptionally resilient and potentially productive species, capable of adapting to various changes in the current environment, even when they do not align with its specific ecological requirements. Nevertheless, *P. tomentosa*'s high carbon use efficiency compared to the native experimental species suggests its potential invasiveness.

Key words: carbon use efficiency, dark respiration, environmental stressors, light-saturated photosynthesis, light use efficiency.

Introduction

The photosynthetic activity of plants is highly correlated with solar radiation and thus net carbon gain and biomass production, if other factors are optimal, such as water and nutrient supply. The survival and growth of plants rely on their carbon balance. Two significant flows primarily govern the carbon balance of vegetation: the input of carbon through photosynthesis and the output through respiration. The value of daily whole-plant gross CO_2 assimilation is positively correlated with growth irradiance and there is supporting evidence indicating an irradiance-dependent relationship with respiration, as well (Pons and Poorter 2014). Achieving

the maximum net photosynthetic carbon gain relies significantly on acclimating leaf physiological traits (Björkman 1981, Givnish 1988) as a vital strategy.

Species adapted to high irradiance, which are shade-intolerant, tend to invest significantly in leaf traits that maximize the photosynthetic rate and photoprotective mechanisms, relative to those associated with light absorption (Valladares and Niinemets 2008, Dusenge et al. 2015, Anev and Marinova 2021). Schulze et al. (2002) indicated that when plotting the rate of photosynthesis in relation to increasing light, the initial slope of the light response curve is linear before the rate levels off and becomes constant as photosynthesis saturates. Excessive light can be absorbed by chloroplasts but may not be effectively utilized for assimilation, fluorescence or dissipation as heat, potentially causing severe oxidative stress. Hight leaf temperatures can lead to stomatal closure and limited photosynthesis (Yamori 2016).

In low light environments, photon absorption becomes a limiting factor for photosynthetic rates. As a result, shade-tolerant species proportionally invest more in structural components and pigments, leading to greater light absorption compared to shade-intolerant species (Feng et al. 2004, Valladares and Niinemets 2008). Within a species, plants grown in shaded locations, as opposed to those growing in well-lit environments, tend to have leaves with a low dark respiration rate, light-compensation point, light-saturation point, net photosynthetic rate, and electron transport rate, primarily due to the low concentration of photosynthetic enzymes in the leaves (Craine and Reich 2005, Valladares and Niinemets 2008, Kolev and Anev 2022). These shade-tolerant plants achieve their maximum rates of photosynthesis at lower light intensities and may also photosynthesize more efficiently at low light levels, although this efficiency aspect is less well-established (Baker 1950). The research conducted by Kubiske and Pregitzer (1996) demonstrated that the alterations induced by various levels of CO_2, which gas is significantly elevated in an urban environment (Liu et al. 2011), in the parameters associated with how plants respond to light interacted in a manner that resulted in distinct predictions for the carbon balance at the leaf level, especially under different light conditions. Notably, these effects of shade were most prominent in plant species that possess a high degree of shade tolerance. Bazzaz and Carlson (1982) observed in their study that late-successional species demonstrated greater CO_2-induced growth enhancements in shade compared to full sun conditions. Additionally, Takagi and Gyokusen (2004) indicated that in their study the shade-tolerant species *Ilex rotunda* showed high photosynthetic performance under low photosynthetic active radiation. On the other hand, Kjelgren and Clark (1992) found a reduction in photosynthesis of shade-intolerant species *Liquidambar styraciflua* L. due to shadowing by tall buildings. However, it should be emphasized that *Liquidambar styraciflua* L. and *Ilex rotunda* Thunb. have different light requirements. The varying physiological responses of tree species to light conditions, which are influenced by their ecotype, states that appropriate selection of tree species can therefore change potential stress factors into favourable conditions.

The study of physiological response to light shows the current state of the experimental trees and their potential for adaptation under urban environmental conditions. However, there are few studies on the effects of the urban microenvironment

on trees (Bassuk and Whitlow 1987, Whitlow and Bassuk 1988, Takagi and Gyokusen 2004, Anev 2016, Wang et al. 2019). Fortunately, advanced instruments, such as infrared portable gas analysers, allow more photosynthetic parameters to be measured in the field. We aimed to investigate the various responses of the photosynthetic parameters in different tree species to the urban environment to provide references for improving the growth conditions of the trees in the cities. We anticipated that each tree species would exhibit distinct light curves, reflecting the fine details of their adaptation to the challenging conditions of an urban environment.

Materials and Methods

In June 2023, a field experiment was conducted on the territory of the University of Forestry located next to the large boulevard St. Kliment Ohridski in the city of Sofia, Bulgaria (42°41'57" N, 023°19'21" E). The area is in the temperate climate zone and has a humid continental climate with warm summers – average monthly temperatures fall below 0 °C and do not exceed 22 °C, with more than 3 months having an average temperature above 10 °C. The mean annual temperature is 10.6 °C, and the mean annual precipitation is 581.8 mm, reaching its maximum in late spring and early summer when thunderstorms are not uncommon (NOAA 2021). The average monthly June temperature was 18.5 °C, the average monthly June precipitation was 161.4 mm (NIMH 2023).

Seven tree species used for landscaping were selected: *Ailanthus altissima* Swingle, *Betula pendula* Roth, *Paulownia tomentosa* Siebold & Zucc, *Quercus robur* L., *Tilia cordata* Mill., *Tilia platyphyllos* Scop. and *Tilia tomentosa* Moench for the measurements. The age of the trees in the study ranged from 40 to 60 years. Apart from *P. tomentosa*, all experimental trees are located within the yard, positioned between the two university buildings. In contrast, *P. tomentosa* is situated independently near a small building adjacent to the park area.

Gas-exchange measurements were made using a portable photosynthesis system (LI-6400®, LI-COR, Lincoln, NE, USA) with an infrared gas analyser (IRGA) connected to a 6400-02B measuring chamber with a LED light source. During the measurements, we strictly adhered to the PrometheusWiki Gold Leaf Protocol (Evans and Santiago 2014). This protocol provides detailed instructions on how to perform basic measurements using the LI-COR 6400 gas exchange instrument. The measurements of net photosynthesis in response to photosynthetic photon flux density (PPFD) were conducted on sunny days, between 10:00 and 13:00. The measurements were carried out *in situ* by collecting three branches from various exposures of the middle section of the crown of each of the studied tree individuals. From each branch, the third leaf, counting from the tip of the branch, was chosen for the measurements (Evans and Santiago 2014). The leaves were exposed to ambient CO_2 levels and saturating PPFD conditions, set at 2000 μmolγ·m^{-2}·s^{-1}, until both net photosynthesis and intercellular CO_2 concentration had stabilized. The time provided for leaf adaptation when PPFD changes was between 60 and 120 s. Subsequently, the PPFD was systematically reduced in incremental steps, including 2000, 1000, 500, 250, 100, 50, 25 and 0 μmolγ·m^{-2}·s^{-1} changed by the auto program 'Light_curve'. Net photosynthesis was recorded at each of these PPFD levels once the leaves had reached a steady-

state condition, as described earlier.

The results of the measurements for the light curves from each species were processed using a special software – Photosynthesis tool, which regressively smooths the light dependence of photosynthesis according to the model described in Li-Cor Application Note #105 (Norman et al. 1991) to determine some physiological parameters of the experimental trees, such as light-saturated photosynthesis (A_{max}), dark respiration (R_d) and light use efficiency (LUE). Carbon use efficiency (CUE) was calculated as the ratio of light-saturated photosynthesis to dark respiration. One-way ANOVA tests and Tukey post hoc analysis were performed to determine the difference between the average values of A_{max}, R_d, LUE, and CUE.

Results and Discussion

This study investigated the impact of fluctuations in photon flux density on the parameters of the light photosynthetic curve for various trees used in urban landscaping (Fig. 1).

The response of tree species to changes in light can be observed through the analysis of generalized parameters of light curves.

Light-saturated photosynthesis

We observed (Fig. 2) significant differences in the light-saturated photosynthesis among the studied tree species, indicating substantial variations in their photosynthetic capabilities (one-way ANOVA, $F = 12.843$, $P < 0.001$). *Q. robur* has the highest levels of A_{max} compared to the other experimental species. The other tree species in the experiment also have a high light-saturated photosynthesis rate, although not as high as that of *Q. robur.* Among them, *T. cordata* stands out, which has significantly higher light-saturated photosynthesis than *P. tomentosa* and *T. tomentosa* and similar levels of A_{max} to *A. altissima* and *B. pendula*.

Q. robur biological features (tall, long-lived, forming large and spread crown) and ecological needs (shade-intolerant) are a prerequisite for reaching high levels of photosynthesis under suitable environmental conditions (Schulze et al. 2006). Elevated nocturnal temperatures in the cities can also stimulate night-time respiration in some trees, which can lead to increased photosynthesis the following day (Turnbull et al. 2002). In our study, *Q. robur* demonstrated a higher assimilation rate compared to previous research (Čater and Levanič 2015, Gardner et al. 2021) findings. The high A_{max} observed in *Q. robur* could be also attributed to the beneficial effects of increasing carbon dioxide levels in urban environments (Kubiske and Pregitzer 1996, Liu et al. 2011) on photosynthesis. Such results indicate that the lighting conditions for *Q. robur* are conducive to supporting intense photosynthesis. Likewise, Lukowski and all. 2020 find in their study that *Q. robur* exhibits better resistance to air pollutants compared to other tree species studied in our experiment, which aids in mitigating the negative impact of these pollutants on photosynthesis rates.

It is interesting that in our study *T. cordata*, which is commonly acknowledged as a shade-tolerant species (Pigott 1991, Eaton et al. 2016), which characterizes it with a lower photosynthetic capacity than shade-intolerant species (Mathur et al. 2018), has similar levels of A_{max} to the

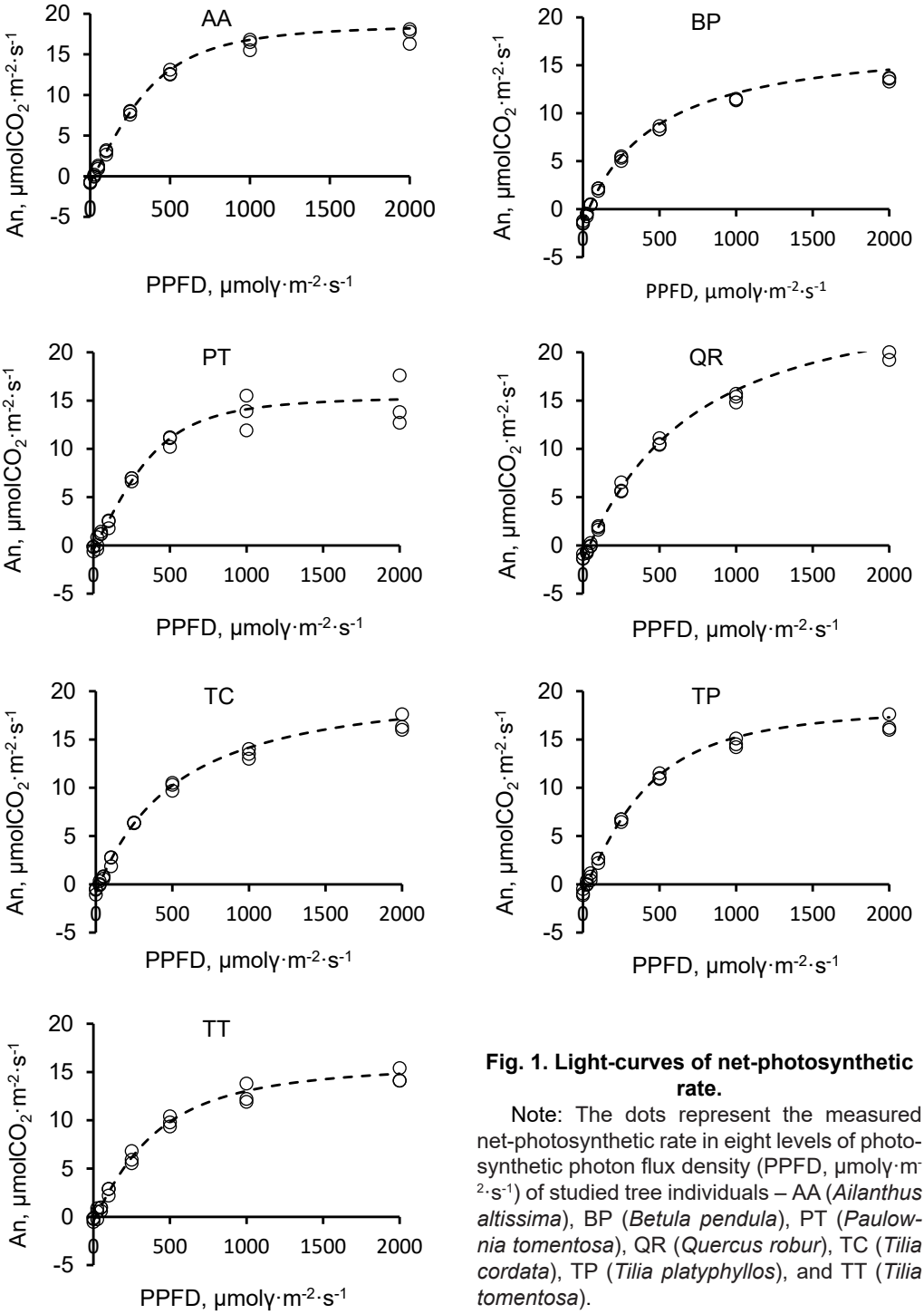

Fig. 1. Light-curves of net-photosynthetic rate.

Note: The dots represent the measured net-photosynthetic rate in eight levels of photosynthetic photon flux density (PPFD, μmolγ·m^{-2}·s^{-1}) of studied tree individuals – AA (*Ailanthus altissima*), BP (*Betula pendula*), PT (*Paulownia tomentosa*), QR (*Quercus robur*), TC (*Tilia cordata*), TP (*Tilia platyphyllos*), and TT (*Tilia tomentosa*).

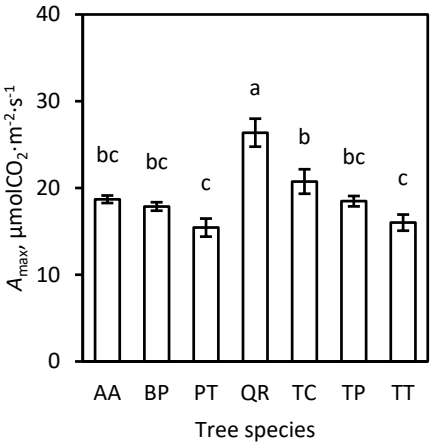

Fig. 2. Light-saturated photosynthesis.

Note: The letters below the columns represent the studied tree individuals – AA (*Ailanthus altissima*), BP (*Betula pendula*), PT (*Paulownia tomentosa*), QR (*Quercus robur*), TC (*Tilia cordata*), TP (*Tilia platyphyllos*), and TT (*Tilia tomentosa*). The columns are the average light-saturated photosynthesis (A_{max}) measured from the leaves of each tree species. The whiskers represent the standard error. The different letter denotes statistically significant difference averages among objects (one-way ANOVA using Tukey post hoc tests with $\alpha = 0.05$).

shade-intolerant tree species in the experiment (*A. altissima* and *B. pendula*) (Beck et al. 2016, Knusel et al. 2016) except for shade-intolerant *Q. robur* (Ellenberg 1988) and even higher A_{max} than moderately shade-tolerant *T. tomentosa* (Radoglou et al. 2009) and shade-intolerant *P. tomentosa*. Proceeding from the fact that shade-tolerant plants achieve their maximum rates of photosynthesis at lower light intensities and may also photosynthesize more efficiently at low light levels (Baker 1950), it can be assumed that this high A_{max} that archives *T. cordata* is probably a result of insufficient solar radiation for intensive photosynthesis in light-loving species, but sufficiently favourable for shade-tolerant ones. *Q. robur*, which is a shade-intolerant tree species, doesn't necessarily invalidate this presumption. In a study by Van Hees (1997), it is observed that when comparing the effects of shading on growth and/or morphology between the shade-tolerant beech and the shade-intolerant pedunculate oak, their responses are surprisingly similar. This suggests that different tree species can exhibit convergent responses to shading conditions, despite their inherent shade tolerance or intolerance characteristics. These findings highlight the complexity of how various tree species adapt to light environments and how their responses may not always align with general expectations based on shade tolerance.

Light use efficiency

No significant differences between experimental tree species were observed in the light-use efficiency (LUE) values (one-way ANOVA, $F = 1.018$, $P = 0.434$) (Fig. 3).

Controversy, Pearcy et al. (2004) found that there were a few significant differences in light capture efficiency among the species in their study. Shade-tolerant plants generally have improved light absorption efficiency than shade-intolerant species (Bongers and Popma 1988, Evans 1989, Kitajima 1994, Kolarov and Tzvetkova 2006). However, in Kim et al. (2008)'s study results, certain *Quercus* species, which are not shade-tolerant species, exhibited an improved ability to absorb and utilize light under low light conditions. Based on the findings from the studies mentioned earlier in our study, the absence of significant differences between experimental tree species may be related to the likely insufficient average monthly solar radiation, which could have equalized the light use efficiency between

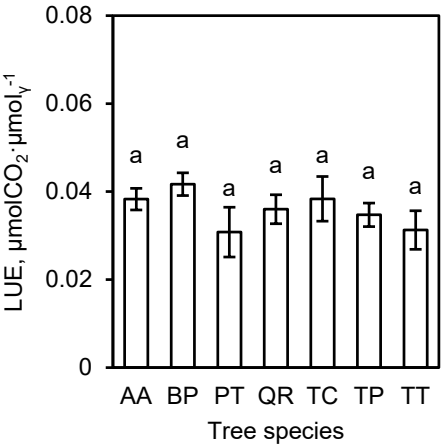

Fig. 3. Light use efficiency.

Note: The letters below the columns represent the studied tree individuals – AA (*Ailanthus altissima*), BP (*Betula pendula*), PT (*Paulownia tomentosa*), QR (*Quercus robur*), TC (*Tilia cordata*), TP (*Tilia platyphyllos*), and TT (*Tilia tomentosa*). The columns are the average LUE from the leaves of each tree species. The whiskers represent the standard error. The different letter denotes statistically significant difference averages among objects (one-way ANOVA using Tukey post hoc tests with $\alpha = 0.05$).

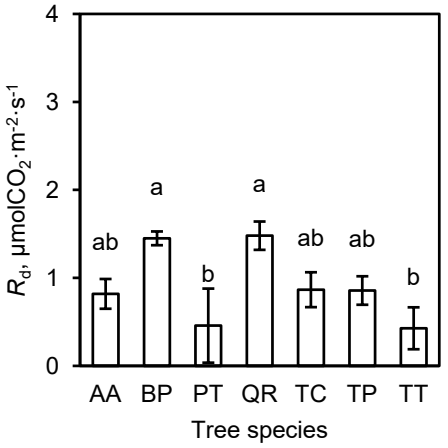

Fig. 4. Dark respiration.

Note: The letters below the columns represent the studied tree individuals – AA (*Ailanthus altissima*), BP (*Betula pendula*), PT (*Paulownia tomentosa*), QR (*Quercus robur*), TC (*Tilia cordata*), TP (*Tilia platyphyllos*), and TT (*Tilia tomentosa*). The columns are the average R_d from the leaves of each tree species. The whiskers represent the standard error. The different letter denotes statistically significant difference averages among objects (one-way ANOVA using Tukey post hoc tests with $\alpha = 0.05$).

the shade-tolerant and shade-intolerant species in the experiment.

Dark respiration

There were notable differences in dark respiration (R_d) when comparing the tree species studied (one-way ANOVA, $F = 3.452$, $P = 0.011$) (Fig. 4). *Q. robur* and *B. pendula* demonstrated significantly higher values of R_d in comparison to *T. tomentosa* and *P. tomentosa*, while the remaining species exhibited similar dark respiration rates.

The higher R_d values of *Q. robur* and *B. pendula* compared to *T. tomentosa* and *P. tomentosa* suggests that *Q. robur* and *B. pendula* may have higher nighttime metabolic activity compared to *T. tomentosa* and *P. tomentosa*. As noted by Turnbull et al. (2002), Kanno et al. (2009) and Searle et al. (2011), elevated night temperature within the city could stimulate respiration and, consequently, photosynthesis. Collalti et al. (2019) observed that the low photosynthetic rates correspond to low respiration rates and the opposite, which we observe in our study, as well. The fact that *B. pendula* does not achieve correspondingly high levels of A_{max} despite having higher R_d rates can be an interesting observation. This suggests that while *B. pendula* may have higher metabolic activity in terms of respiration, it may not be utilizing this higher metabolic activity

to achieve a proportionally higher photosynthetic capacity. The low photosynthesis of *B. pendula* can likely be attributed to air pollutants in the cities, which act as leaf shading and negatively affect photosynthesis of trees (Weber et al. 2002, Przybysz et al. 2014, Popek et al. 2017). Łukowski et al. (2020) indicate that the foliage of *B. pendula* collected a high amount of particulate matter. Dzierżanowski et al. (2011) indicated that in contrast to *Q. robur*, *B. pendula* is more susceptible to air pollutants, particularly of their photosynthetic rates and stomatal conductance (Łukowski et al. 2020). The high intensity of R_d observed in *Q. robur* and *B. pendula* can disrupt carbon balance because plant respiration can release up to about half of the assimilated carbon by photosynthesis daily, as shown by Bruhn (2002). Reduced respiration rates in *T. tomentosa* and *P. tomentosa* are a prerequisite for more efficient carbon assimilation (Griffin et al. 2001, Schulze et al. 2006).

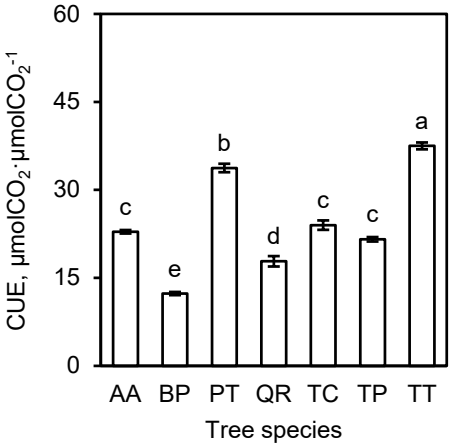

Fig. 5. Carbon use efficiency.

Note: The letters below the columns represent the studied tree individuals – AA (*Ailanthus altissima*), BP (*Betula pendula*), PT (*Paulownia tomentosa*), QR (*Quercus robur*), TC (*Tilia cordata*), TP (*Tilia platyphyllos*), and TT (*Tilia tomentosa*). The columns are the average CUE from the leaves of each tree species. The whiskers represent the standard error. The different letter denotes statistically significant difference averages among objects (one-way ANOVA using Tukey post hoc tests with $\alpha = 0.05$).

Carbon use efficiency

There were significant differences in carbon use efficiency (CUE) when comparing the studied tree species (one-way ANOVA, $F = 203.598$, $P < 0.001$) (Fig. 5). *T. tomentosa* had the highest carbon use efficiency among the studied tree species, followed by *P. tomentosa*. *A. altissima*, *T. cordata*, and *T. platyphyllos* exhibited moderate levels of CUE, while *Q. robur* and *B. pendula* had the lowest values of this indicator.

T. tomentosa and *P. tomentosa* have moderate A_{max} but, at the same time, maintain low R_d, which provides a high CUE. Maintaining a favourable balance of carbon elements means that *T. tomentosa* and *P. tomentosa* capacity to withstand and adapt to the urban light conditions reach higher CUE than all other experimental species, which underscores its resilience, as it remains well-suited to its specific environment and is relatively unaffected by less favourable environment. Compared to *T. tomentosa* and *P. tomentosa, A. altissima*, *T. cordata* and *T. platyphyllos* exhibit moderate levels of carbon use efficiency. Similar to *P. tomentosa*, *A. altissima* does not attain its full photosynthetic potential as a highly shade-intolerant species (Stratton and Goldstein 2001, Lamarque et al. 2011). However, unlike *P. tomentosa*, *A. altissima* does not achieve the same level of balance among its carbon balance elements, resulting in a lower CUE comparable to that

of the shade-tolerant species in the experiment. The lower levels of CUE that *A. altissima* achieves indicates that it is more responsive to environmental conditions and is comparatively more sensitive as a species. The high energy needs of *Q. robur*, resulting from high R_d values, reflects the increased cost element of the carbon balance, leading to the inefficient use of carbon, which lower CUE. Unlike *Q. robur*, *B. pendula* does not exhibit high A_{max} values but shares similar R_d values, which renders it less carbon efficient. Regarding *B. pendula*, its comparatively lower CUE suggests it may face more significant challenges in adapting to the environmental conditions.

Conclusion

Various tree species in our experiment display unique light response curves, which reveal the intricate aspects of their adaptation to the demanding conditions of an urban environment. *B. pendula* is the most shade-intolerant tree species among the native species in the experiment and having low CUE characterizes it as a species that faces comparatively greater challenges in adapting to the environment compared to the other studied species. Despite having the highest rates of A_{max}, the shade-intolerant *Q. robur* also exhibits low CUE, which, similar to *B. pendula*, puts it at a disadvantage for adapting to environmental conditions. *T. platyphyllos*, *T. cordata* and *A. altissima* exhibit moderate CUE. While the light environmental conditions support their presence, their potential for productivity is expected to be comparatively lower than some of the other experimental species. Furthermore, the observation that the shade-intolerant *A. altissima* exhibited comparable CUE to the shade-tolerant species in the experiment suggests that the combination of ecological factors was not conducive for it to fully realize its high photosynthetic potential. It seems that *A. altissima* is more sensitive to the light environmental conditions compared to shade-tolerant *T. platyphyllos* and *T. cordata*. *T. tomentosa* has the most favourable combination of carbon balance components, leading to a high CUE, which designates its environment as conducive to rapid growth and elevated productivity. This suggests that *T. tomentosa* would be a suitable choice for landscaping in an urban environment. *P. tomentosa* also has a high CUE. Even though its photosynthesis rates are relatively lower, possibly due to limited solar radiation, it effectively integrates the components of its carbon balance in a beneficial manner that underscores *P. tomentosa*'s exceptional adaptability to the urban environment, also indicated by other authors (Stojičić et al. 2010, Ivanova et al. 2019, Gyuleva et al. 2021). However, the achievement of almost the highest levels of CUE by the non-native *P. tomentosa* compared to the native experimental species suggests a potentially invasive nature, which landscapers should carefully consider. Conducting a comprehensive study on the response of various tree species to a wider range of ecological factors would be valuable for a more accurate assessment of their ability to adapt to the challenging conditions of an urban environment. Such research could provide valuable insights to assist landscapers in making informed decisions when selecting tree species for landscaping in urban areas.

Acknowledgements

The present study was supported by the national programme 'Young scientists and post-doctoral students – 2' of the Bulgarian Ministry of Education and Science.

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