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Influence of night-time light pollution on the photosynthesis and physiological characteristics of the urban plants *Euonymus japonicus* and *Rosa hybrida*

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Abstract

Background Night-time light pollution (NLP), which breaks the natural cycle of day and night, has become a new threat to urban ecosystems. Plants are the main component of urban ecosystems and play an irreplaceable role in maintaining urban ecological balance. The effects of NLP with various radiation sources, including green, white, blue and red light provided by light-emitting diodes, on urban plants, *Euonymus japonicus* and *Rosa hybrida*, were examined in a block field experiment.

Results NLP caused photoinhibition and oxidative stress in plants, and the extent of the deleterious effects varied with the spectral distribution of artificial light sources and species. Both *E. japonicus* and *R. hybrida* were more sensitive to blue and red light, which reduced the pigment concentration, net photosynthetic rate, stomatal limit value, effective quantum yield, apparent electron transfer rate and photochemical quenching coefficient, and markedly increased the malondialdehyde content and total antioxidant capacity. However, those negative effects under white light were only present in *E. japonicus* and not in *R. hybrida*. Furthermore, blue and red light significantly decreased the stomatal conductance of *E. japonicus*. In contrast, green light had no significant effect on the above indices for both species. All spectra did not significantly change the sugars and starch contents for either species.

Conclusions Considering that the spectral distribution of artificial light at night in cities has great heterogeneity and that its effect varies with plant species, it is important to arrange tree species with NLP tolerance and install appropriate light sources in urban areas based on the corresponding physiological responses and adaptation of urban trees.

Keywords Light pollution, Urban plant, Spectra, Photosynthetic parameter, Physiological characteristics

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Introduction

Light is one of the most essential environmental factors for organisms. As a resource, light can be absorbed by plants and some autotrophs for the photosynthesis, and as a source of information, the intensity, duration and spectral distribution of light have a great influence on organisms' ability to detect diurnal cycles, seasonal changes, and the features of their surrounding environment and regulate their physiological activity (Gaston et al. 2013; Silvestri et al. 2019). Likewise, it has been suggested that continuous periods of darkness play a crucial role in organisms for resources and recovery from environmental stresses, which are experienced by plants during the daytime (Gaston et al. 2013; Singhal et al. 2019). Therefore, the natural pattern of light and dark cycles has been a central contributing factor in the physiology and ecology of organisms. However, since the early twentieth century, as human communities and lighting technologies have developed, dark refuges have been increasingly encroached upon by artificial light at night in space and time (Gaston et al. 2013), resulting in night-time light pollution (NLP) (Falchi et al. 2019). Consequently, the circadian patterns of light and dark, which are closely related to the behavioral patterns of organisms and the timing of ecological processes (Levy et al. 2020), have been disrupted. It has been recently reported that more than 20% of land masses and over 80% of the world's human population are faced with the problem, and areas and populations impacted by NLP are likely to continue to increase in the near future (Falchi et al. 2016; French-Constant et al. 2016; Guan et al. 2022). Many studies highlight that increasing artificial light at night has led to widespread concern over the potential ecological impacts of NLP (Barre et al. 2021; Gaston et al. 2013; Haddock et al. 2019). Most of the earlier studies have mainly focused on investigating the effects of NLP on the animal system and ecosystem sustainability, but very few studies have paid attention to the plant system (Haddock et al. 2019; Singhal et al. 2019).

As a result of evolution, plants develop a great deal of complex pigment systems to absorb certain wavelengths of the light spectrum (Singhal et al. 2019). In addition to pigment systems, diverse photoreceptors sensing and signaling light for the diurnal regulation of growth and hormonal functions have also developed (Singhal et al. 2019). According to previous studies, a very short duration or low intensity of light at night is sufficient to cause physiological and behavioral reactions in the plant (Arnott and Macey 1985; Poulin et al. 2014; Raven and Cockell 2006). Artificial light at night may exert a limited impact on the net photosynthesis of plants due to its relatively low quantum flux densities when compared to daylight, but theoretically, artificial light at night,

especially in cave systems, could be sufficient to trigger minimal photosynthesis (Bennie et al. 2016; Raven and Cockell 2006). Moreover, night-time light perceived by phytochromes could disrupt information flow and offer misleading signals affecting the normal signaling and functions of plants (Gaston et al. 2013), which in turn affects their function during the day. The spectral signatures of night-time light vary with different artificial light sources, each of which emits light with different intensities in different wavelength ranges (Gaston et al. 2013). The wavelength of light is essential to its efficacy as an information source due to the different spectral sensitivities of organism receptors (Gaston et al. 2013). Several deleterious effects of NLP have been observed on the physiology of algae and grass (Poulin et al. 2014; Zhang et al. 2020). To date, a few studies on the effects of NLP on vascular plants have mainly focused on phenology (French-Constant et al. 2016; Lian et al. 2021; Massetti 2018), and surprisingly, there is little information about the effects of NLP on the photosynthesis and physiological characteristics of vascular plants.

Urban ecosystems are the most heavily light-polluted areas. As the primary producer of urban ecosystems, vascular plants play an irreplaceable role in maintaining urban ecological balance, improving the urban ecological environment and enhancing human health and quality of life (Wang et al. 2019; Zhang et al. 2021). It is obvious that urban plants are affected by NLP. Therefore, studying the effects of NLP on plants is helpful for ensuring the health and sustainable ecological function of urban ecosystems under the trend of artificial light at night increasing in the future.

Our objective was to evaluate the effects of NLP with different spectra on the photosynthesis and physiological characteristics of urban vascular plants. We selected two landscape plant species *Euonymus japonicus* and *Rosa hybrida* as our model organisms, because they are commonly used for urban greening in Beijing. We hypothesized that NLP would have adverse effects on the photosynthetic and physiological performance of the two species and that those effects varied with spectral distribution and species.

Materials and methods

Experimental design

A controlled experiment was carried out at Tangjiapu Village, Yanqing District, Beijing, China (40° 29' N, 115° 59' E). In August 2021, an experimental area with a size of 36 × 15 m was selected and divided into several experimental plots. Each plot was 2 × 2 m, and there was a 1.5 m margin between plots. In April 2022, 15 plots were selected and allocated to five treatments (three replicates per treatment). Light treatments with green,

white (Correlated Color Temperature, 6500 K), blue and red LEDs, respectively, mounted 1.7 m above the ground on a wooden frame in the center of the plot were added to these 12 plots to provide night-time light. The spectral composition was determined by a spectrometer (AVANTES, Netherlands) (Additional file 1: Fig. S1). The mean light intensities of the green, white, blue, and red LEDs measured by the illuminometer (XIMA, China) on the ground of the plots were 35.78, 37.33, 36.29 and 39.03 lx, respectively, which were below $1 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. The irradiation time of the LED lamps was controlled by a light-sensitive switch to turn on at dusk and off at dawn. In the remaining three plots, no lighting equipment was installed, so they were not affected by night-time light. The illuminance in the ambient environment was close to 0 lx when there was no moonlight. See Additional file 1: Fig. S2 for images of the field experiment at dawn and at night.

In addition, in April 2022, 2-year-old *E. japonicus* and *R. hybrida* plants with mean heights of 77.37 cm and 60.73 cm, respectively, and basal diameters of 14.62 mm and 13.27 mm, respectively, were purchased from a plant nursery. Then, 90 *E. japonicus* plants and 90 *R. hybrida* plants were randomly divided equally among the 15 plots and planted directly into the soil. During the whole experiment, all plants were fully watered and fertilized. Briefly, there were 5 treatments: no light (CK), green, white, blue and red. For each treatment and plant species, there were three plots as replicates, and each plot had six plants.

Measurements of gas exchange and chlorophyll fluorescence parameters

For either species in each plot, two mature leaves from the tops of two different plants were chosen in middle of August 2022. Gas exchange and chlorophyll fluorescence parameters were measured on sunny windless mornings from 8:30 to 11:30 using a portable photosynthesis analyzer (LI-6400XT, LI-COR, Lincoln, NE, USA) equipped with a fluorescent leaf chamber. During the measurements, photosynthetically active radiation was $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$, which is close to the saturation light intensity of the two species, the gas flow rate was set to 500 mmol s^{-1} , and CO_2 was provided by a buffer bottle placed away from the measuring point to keep a stable CO_2 input equal to the background level. When the instrument was stable the following parameters were determined. Gas exchange parameters: net photosynthetic rate (P_n , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), stomatal conductance (G_s , $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$), and stomatal limit value (L_s); Chlorophyll fluorescence parameters: effective quantum

yield (Φ_{PSII}), apparent electron transfer rate (ETR), and photochemical quenching coefficient (q_p).

Measurements of photosynthetic pigments

Leaf samples were collected using a hole punch with a 0.7 cm diameter from the leaves that had been measured by the LI-6400XT. Chlorophyll and carotenoids were extracted in a centrifuge tube with 5 mL of 95% ethanol in the dark. The extracting solution was measured at 470, 649 and 665 nm by a UV spectrophotometer (Agilent, USA), and the chlorophyll a (Chla), chlorophyll b (Chlb) and carotenoids contents were calculated using the equations described by Lichtenthaler and Wellburn (1982). The values of chlorophyll a + b (Chla + b) and chlorophyll a/b (Chla/b) were then calculated.

Measurements of malondialdehyde (MDA), total antioxidant capacity (TAC), sugars and starch

For either species, two plants in each plot were chosen, and ten mature leaves in the upper part of either plant were sampled from the chosen plants in the morning in late August. The collected leaves were divided into two parts. One part of the samples was immediately frozen in liquid nitrogen and stored in an ultralow temperature freezer for the determination of MDA and TAC, and the other part was dried in an oven at 70°C for the determination of sugars and starch contents. The relevant measurement methods are below.

MDA: The method described by Heath and Packer (1965) was modified appropriately to determine MDA contents. A 0.07 g sample was ground in a grinding bowl, and then 4 ml of 10% trichloroacetic acid was added and ground into a homogenate. The homogenate was poured into a centrifuge tube and centrifuged at $12,000 \times g$ for 3 min. Two milliliters of the extract was collected and mixed with 2 ml of 0.6% thiobarbituric acid. The mixture was heated in a 100°C water bath for 15 min. The reaction was then terminated by rapid cooling. The mixture was centrifuged at $12,000 \times g$ for 3 min, and then the supernatant was collected. The light absorption values of the supernatant at 450, 532 and 600 nm were measured by the spectrophotometer.

TAC: The method described by Benzie and Strain (1996) was modified appropriately to determine TAC. A 0.06 g sample was ground in a grinding bowl, and then 4 ml of 70% ethanol was added for grinding until homogenization. The homogenate was poured into a centrifuge tube and centrifuged at $12,000 \times g$ for 3 min. Then, 100 μl of the extract was collected, and 5 ml of FRAP reaction solution was added. The mixture was centrifuged at $12,000 \times g$ for 3 min, and then the supernatant was collected. The absorption value of the supernatant at 593 nm was determined by the spectrophotometer. The

total antioxidant capacity of the sample was expressed as equivalent to the reducing power of Fe^{2+} .

Sugars: The method described by Fairbairn (1953) was modified appropriately to determine sugars. A 0.1 g sample was ground in a grinding bowl, and then 4 ml of 80% ethanol was added to grind until homogenization. The homogenized sample was poured into a test tube, heated in a water bath at 80 °C for 40 min, poured into a centrifuge tube, and centrifuged at $12,000 \times g$ for 3 min, and the supernatant was collected. The process was repeated twice, and the supernatant was recovered. Next, 10 mg of activated carbon was added to the supernatant for decolorization at 80 °C for 30 min. After the supernatant was filtered, 100 μl of supernatant was collected, 5 ml of anthrone reagent was added, and its light absorption value at 625 nm was determined by the spectrophotometer.

Starch: The method described by Clegg (1956) was modified appropriately to determine the starch contents. The residue after extracting sugars was transferred to a volumetric flask, and 5 ml of water was added. Then, it was heated in a water bath at 100 °C for 15 min. Then, 2 ml of 9.2 mol/L perchloric acid was added to the volumetric flask, and the heating continued for 5 min. After the reaction, the mixture was centrifuged at $12,000 \times g$ for 3 min, and the supernatant was collected. This process was repeated twice, and the supernatants were combined. The supernatant was determined according to the method used to determine sugars.

Statistical analysis

Statistically significant differences among treatments were determined using one-way analysis of variance (ANOVA) followed by the LSD test for multiple comparisons. The correlations between P_n and the biochemical index and other photosynthetic parameters were determined using Pearson's correlation test. Before statistical analysis, the homogeneity of the variance and normality of distribution of data were tested, and logarithmic transformation was carried out for data that did not meet the above conditions. All statistical analyses were performed using the IBM SPSS Statistics Version 22 software package, and the graphics were drawn with Origin software.

Results

Photosynthetic pigments

As shown in Fig. 1, compared with the CK treatment, the Green treatment did not significantly change the pigment contents in either species. The Chla, Chlb, Chla+b and carotenoids contents decreased significantly in the White, Blue and Red treatments in comparison with the CK treatment for *E. japonicus*, and the effects of the Blue and Red treatments were significantly

greater than those of the White treatment. The negative effects on Chla, Chlb, Chla+b and carotenoids only occurred in the Blue and Red treatments, and not in the White treatment, for *R. hybrida*. No significant difference in pigment content was found between the Blue and Red treatments for either species. All night spectra did not significantly change the value of Chla/b.

Gas exchange parameters and fluorescence parameters

The gas exchange parameters and fluorescence parameters in the leaves of *E. japonicus* and *R. hybrida* in different light treatments are presented in Fig. 2. When compared with the CK treatment, for both *E. japonicus* and *R. hybrida*, the values of P_n , L_s , Φ_{PSII} , ETR and q_p decreased significantly in the Blue and Red treatments, and these values were not significantly different in the Green treatment. Negative effects of the White treatment occurred on P_n , L_s , Φ_{PSII} , ETR and q_p only for *E. japonicus* and not for *R. hybrida* in comparison with CK. Compared with the White treatment, the values of P_n decreased significantly in the Blue and Red treatments, and the values of Φ_{PSII} and ETR decreased significantly in the Blue treatment but not in the Red treatment for *E. japonicus*. Compared with the other treatments, a decreased G_s appeared only in the Blue and Red treatments of *E. japonicus*. Furthermore, there was no significant difference between the Blue and Red treatments in all of the above parameters for both *E. japonicus* and *R. hybrida*.

MDA, TAC, sugars and starch

Compared with the CK treatment, the Green treatment did not significantly change the MDA and TAC contents in either species (Fig. 3a, b). MDA and TAC increased significantly in the White, Blue and Red treatments for *E. japonicus* in comparison with the CK, and the effects of the Blue and Red treatments were significantly greater than those of the White treatment. The effects on MDA and TAC only occurred in the Blue and Red treatments, not in the White treatment, for *R. hybrida*. There was no significant difference between the Blue and Red treatments in MDA and TAC for both *E. japonicus* and *R. hybrida*. In contrast, the sugars and starch contents were not significantly changed in any of the treatments for the two species (Fig. 3c, d).

Correlation coefficients between P_n and photosynthetic and physiological parameters

The P_n was significantly positively correlated with Chla, Chlb, Chla+b, carotenoids, L_s , Φ_{PSII} , ETR and q_p , but significantly negatively correlated with MDA and TAC

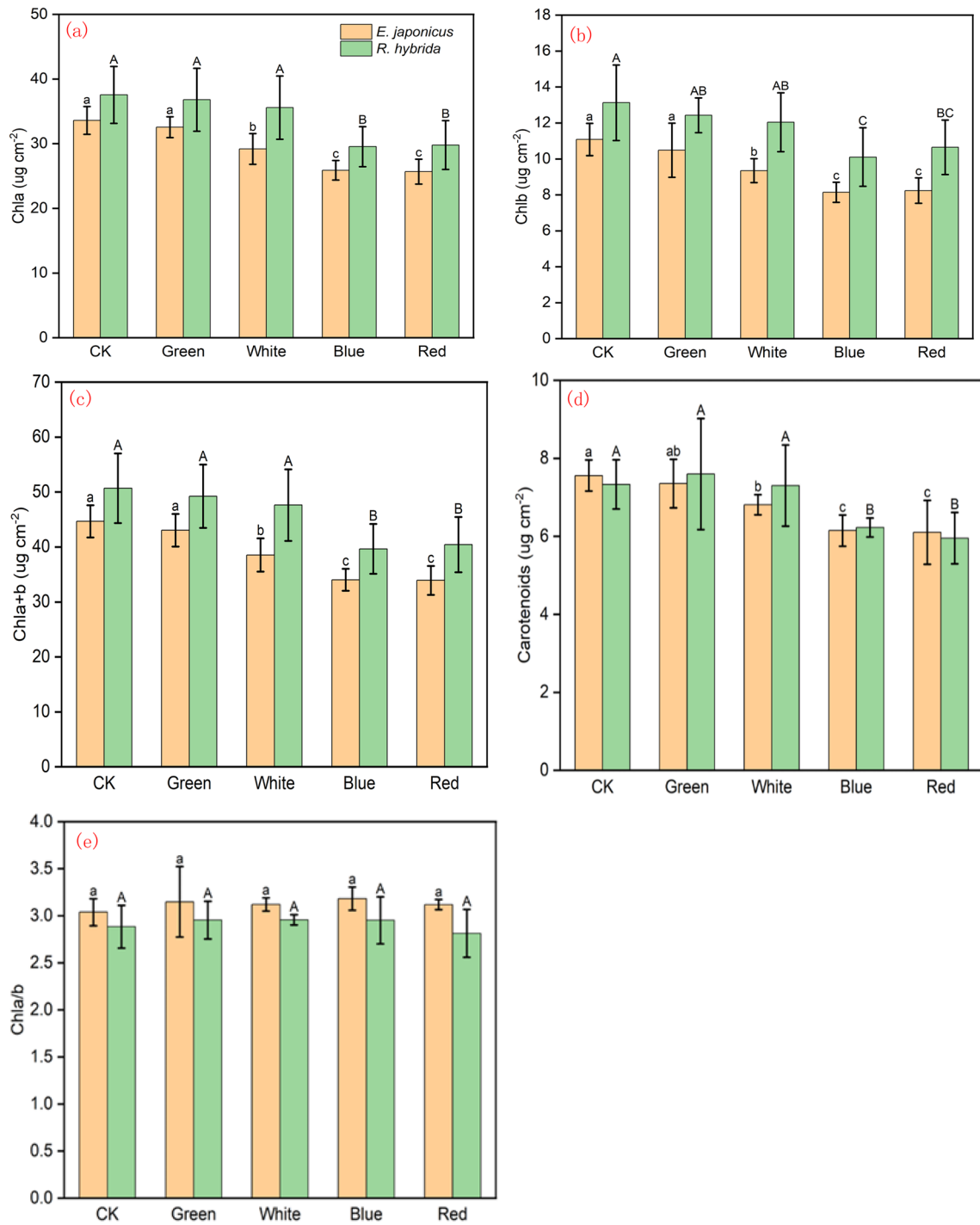


Fig. 1 Contents of Chla (a), Chlb (b), Chla+b (c) and carotenoids (d) and the Chla/b ratio (e) in *E. japonicus* and *R. hybrida* in different light treatments. Different lowercase and capital letters above the bars indicate significant differences among the light treatments at $p < 0.05$ for *E. japonicus* and *R. hybrida*, respectively. The data are the mean values \pm SDs

for both *E. japonicus* and *R. hybrida* (Table 1). However, Chla/b, sugars and starch had no significant correlations with P_n for either species. In addition, the significantly

positive relationship between P_n and G_s only occurred in *E. japonicus*, but not in *R. hybrida*.

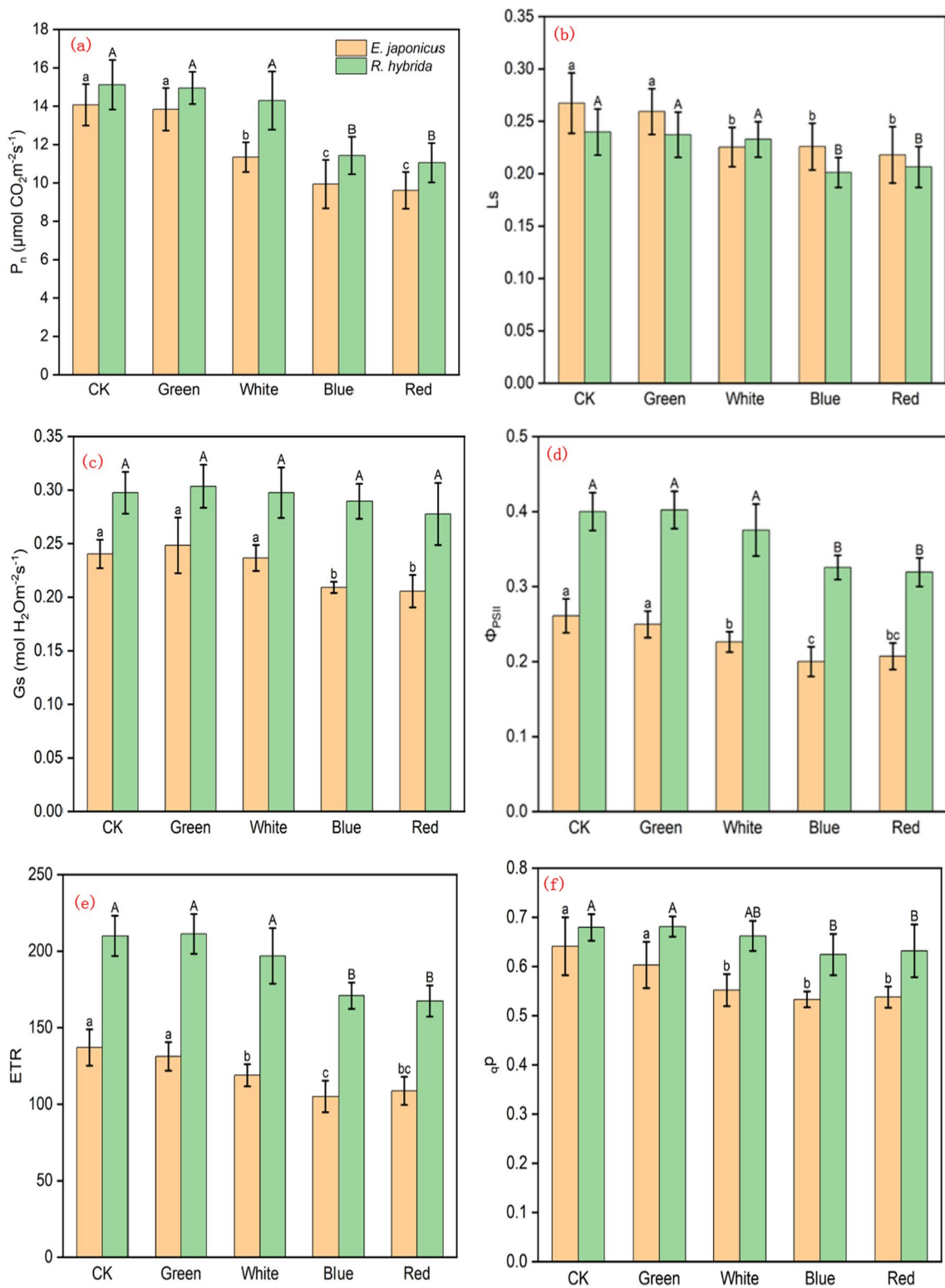


Fig. 2 Values of P_n (a), L_s (b), G_s (c), Φ_{PSII} (d), ETR (e) and q_p (f) in *E. japonicus* and *R. hybrida* in different light treatments. Different lowercase and capital letters above the bars indicate significant differences among the light treatments at $p < 0.05$ for *E. japonicus* and *R. hybrida*, respectively. The data are the mean values \pm SDs

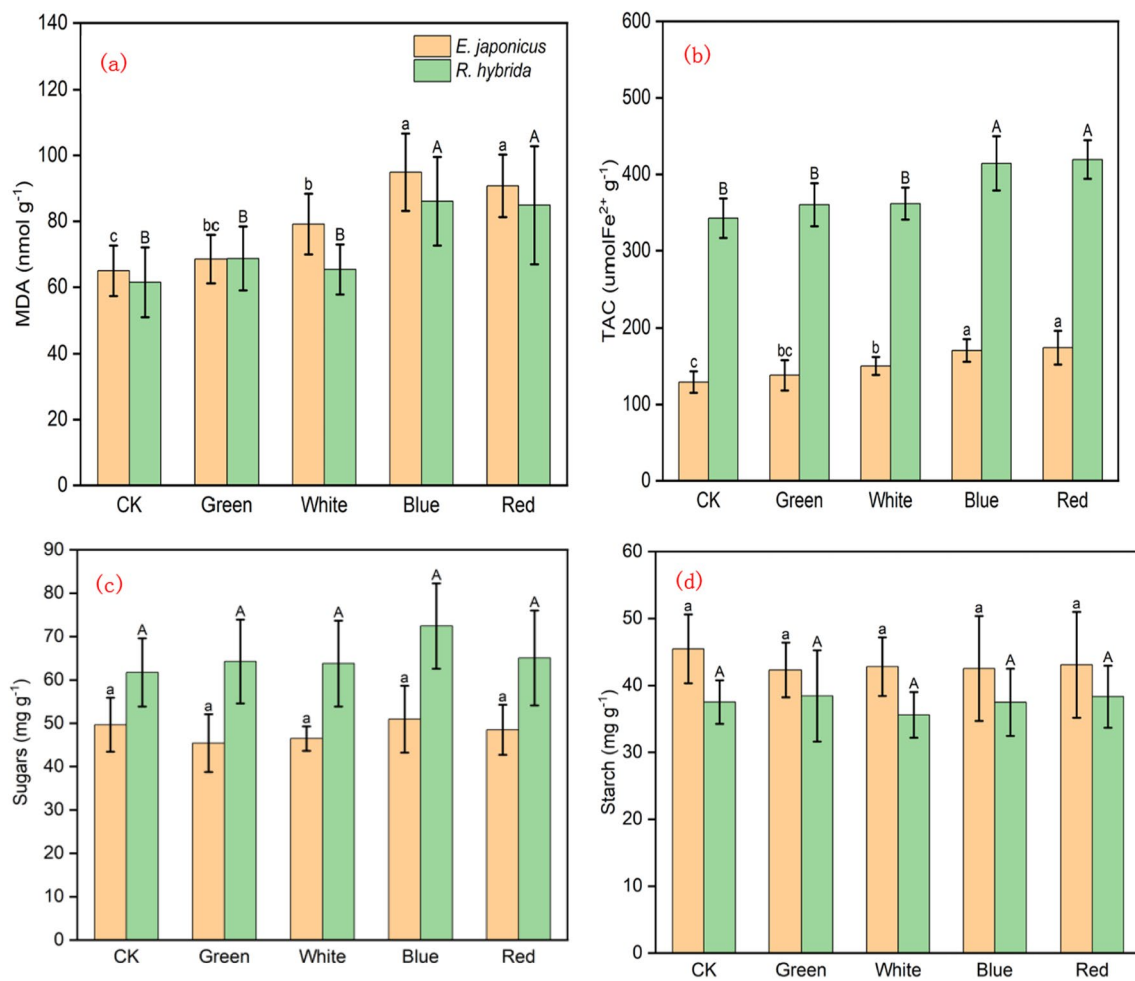


Fig. 3 Contents of MDA (a), TAC (b), sugars (c) and starch (d) in *E. japonicus* and *R. hybrida* in different light treatments. Different lowercase and capital letters above the bars indicate significant differences among the light treatments at $p < 0.05$ for *E. japonicus* and *R. hybrida*, respectively. The data are the mean values \pm SDs

Discussion

As an adverse environmental stress, NLP, which disrupts the diurnal cycle, is achievable with the use of artificial light sources. There is an immense difference in spectral distribution between artificial light and solar light, and the relationships between light sources with different spectral distributions and the induced effect of continuous light in plants are complicated (Velez-Ramirez et al. 2011). To date, no conclusive links can yet be made for the responses of plants under NLP. A key challenge for NLP research is to determine the spectral distribution and intensity of plants exposed to artificial light at night, which differs greatly within a small geographical scale and is even unknown for some environments (Levy et al. 2020). The effects of NLP vary with plant species, which is another difficulty. In the current study, different light spectra below $1 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ were employed, which is within the light intensities experienced under

urban artificial lighting sources (Bennie et al. 2016). In our study, both *E. japonicus* and *R. hybrida* experienced more severe oxidative stress conditions, together with a significant decrease in the pigment contents and the values of P_n , L_s , Φ_{PSII} , ETR, and q_p and a significant increase in the contents of MDA and TAC under blue and red light. Many studies have shown that the effects of blue and red light were more capable of causing visible changes than other wavebands (Wang and Folta 2013), which is consistent with our research. Furthermore, the negative effects caused by white light only occurred in *E. japonicus* and not in *R. hybrida*, indicating that the effect of NLP on plants is affected by species. Compared with *E. japonicus*, *R. hybrida* has a stronger antioxidant capacity, which may be more resistant to the stress caused by NLP. Although plants have a limited ability to absorb green light during photosynthesis, green light can still be perceived by plants as a light signal, thus regulating

Table 1 Pearson's correlation coefficients between P_n and the photosynthetic and physiological parameters of *E. japonicus* and *R. hybrida*

Index	<i>E. japonicus</i> P_n	<i>R. hybrida</i>
Chla	0.843**	0.597**
Chlb	0.767**	0.534**
Chla+b	0.833**	0.592**
Carotenoids	0.699**	0.511**
Chla/b	-0.153	0.090
L_s	0.845**	0.839**
G_s	0.581**	0.361
Φ_{PSII}	0.720**	0.711**
ETR	0.721**	0.711**
qP	0.630**	0.407*
MDA	-0.694**	-0.670**
TAC	-0.711**	-0.647**
Sugars	-0.103	-0.071
Starch	0.219	-0.048

Significance levels: ** $P < 0.01$, * $P < 0.05$. No asterisks indicate the absence of a significant relationship

plant growth and development. Recently, it was found that green light can drive periodic changes in bioluminescent circadian rhythm reporter genes (*CCA1::LUC2* or *TOC1::LUC*) in transgenic plants, and further studies have shown that green light can activate Cry1-mediated circadian rhythm regulation (Battle and Jones 2020; Jin et al. 2020). However, the photosynthesis and physiological characteristics of both species did not change significantly in the Green treatment, which may be because the light intensity in our experiment was too low to detect the signal for the plant. The specific biological mechanism needs to be further explored to explain the reason.

Faced with stresses, plants adapt to adversity by changing their appearance, morphological structure and biochemical metabolic activities (Gilbert and Medina 2016). In our research, the decreased pigment contents under NLP were similar to those in some previous studies (Haque et al. 2015; Zhang et al. 2020). In general, photooxidation might cause a reduction in pigment content under continuous light. In addition, the reduction in pigment content is regarded as a pressure response mechanism to decrease light absorption by chloroplasts. Haque et al. (2015) reported a higher Chla/b ratio in *Solanum pimpinellifolium* under continuous light, indicating that this species was more efficient in adapting to continuous light, possibly by decreasing the light-harvesting chlorophyll-protein complexes. However, no difference in Chla/b was found among all the treatments for both species, suggesting that there is a photoprotective

mechanism for these two species to maintain photosynthetic system stability even under NLP stress.

The decrease in the photosynthetic rate under environmental stress is mainly caused by stomatal and non-stomatal factors. When photosynthesis decreases, if L_s increases, the photosynthetic rate is mainly attributed to stomatal factors; if L_s decreases, the decrease in the photosynthetic rate is mainly controlled by nonstomatal factors (Wang et al. 2019). In our research, the P_n and L_s of *E. japonicus* decreased significantly under the White, Blue and Red treatments, and these values of *R. hybrida* decreased significantly under the Blue and Red treatments, which was consistent with the nonstomatal limitation mainly associated with photoinhibition. Photoinhibition refers to the phenomenon that the activity of photosystem II (PSII) is inhibited when photosynthetic organisms are exposed to unfavorable or stressful environmental conditions (Aro et al. 1993; Murata et al. 2007). Electron transport, the synthesis of ATP and NADPH, and the catalysis of Rubisco can be restrained by unfavorable or stressful environmental conditions leading to excessive reactive oxygen species (ROS), which in turn accelerates photodamage to PSII and inhibits its repair (Allakhverdiev et al. 2005; Murata et al. 2007). We also found that the G_s of *E. japonicus* decreased significantly under the Blue and Red treatments, suggesting that blue and red light affected the stomatal function of *E. japonicus*. Studies have shown that continuous light interferes with the normal movement of stomata and reduces stomatal size and apertures, resulting in a decline in stomatal conductance, thus limiting CO_2 availability for photosynthesis, and causing a decrease in NADPH and P_n .

It is helpful to determine the efficiency of energy transfer in PSII by studying the fluorescence properties of chlorophyll molecules, and fluorescence measurement is an important measure to investigate photosynthesis without damage (Ball et al. 1994). Φ_{PSII} indicates the proportion of absorbed energy used in photochemical reactions, and ETR is an empirical estimate of the rate of flow of electrons through the electron transport chain (Park and Dinh 2019). The values of Φ_{PSII} and ETR in *E. japonicus* with the White, Blue and Red treatments and *R. hybrida* with the Blue and Red treatments decreased significantly, showing that PSII was damaged and the ability to capture and transfer electrons in their leaves was reduced. The plant is sensitive to night-time light, and extremely low photosynthetic quantum flux can cause a significant effect on plant physiology (Poulin et al. 2014; Raven and Cockell 2006). The dark phase of the diurnal cycle is replaced by NLP. As a result, an environment in which the natural night-time brightness has been changed is created. Under this condition, plants face pressure due to

the changed light pattern, and ROS are produced accordingly, which in turn prevents the repair of photodamaged PSII by suppressing primarily the synthesis of proteins (Murata et al. 2007; Velez-Ramirez et al. 2011). The value of q_p represents the energy used by photosynthesis, and the decrease of it in the study indicated that there was more absorbed light dissipating by a thermal reaction and not by a photochemical reaction under NLP (Wang et al. 2019). In this experiment, the significant reduction in pigment contents and the values of Φ_{PSII} , ETR and q_p attributed to photoinhibition were important factors in the decline in P_n (Table 1).

Plants would produce more ROS when facing certain stresses, and the major damaging effect is the peroxidation of membrane lipids. MDA is the final decomposition product of membrane lipid peroxidation (Zhang et al. 2020), and the overaccumulation of MDA in continuous light might damage the ultrastructure and function of chloroplasts and affect PSII activity and photosynthetic pigments (Haque et al. 2015). In this research, MDA and TAC significantly increased in the White, Blue and Red treatments for *E. japonicus* and in the Blue and Red treatments for *R. hybrida*, illustrating that excessive ROS production under NLP stimulated the antioxidant machinery, which may reduce the photosynthetic rate of the plant (Table 1). In addition, NLP has been found to increase MDA in *Lolium perenne* (Zhang et al. 2020). As a resource for plant growth and some physiological processes, a period of darkness is crucial for plant repair and recovery from environmental stresses. The balance of day and night is disrupted by NLP, which significantly increases photooxidative pressure. Normally, the content of ROS in plant cells is in a dynamic equilibrium (Zhang et al. 2019). During the evolution process, a perfect defense system has been developed in plants to address this negative effect. Plants can improve their antioxidant capacity to reduce the content of ROS and maintain the normal physiological function of cells under stress (Levy et al. 2020). However, in the current study, this antioxidant capacity was not sufficient to counteract the high occurrence of lipid peroxidation (Levy et al. 2020), causing a higher MDA level.

Sugars and starch are important components of non-structural carbohydrates (NSCs) in plants and are related to a variety of physiological functions (Resco de Dios and Gessler 2021). Various metabolic fluxes are regulated by diurnal cycles in plants to adapt to diverse environmental conditions (Singhal et al. 2019). During the day, stomata in plants are opened, CO_2 is fixed and NSCs are accumulated; at night, stomata close, carbon fixation stops, and the accumulated NSCs support plant metabolism until the next morning (Velez-Ramirez et al. 2011). By inhibiting starch-degrading enzymes, continuous light

can decrease carbohydrate export from the leaf, leading to higher NSCs in leaves (Haque et al. 2015). However, in our study, sugars and starch contents in the leaves of *E. japonicus* and *R. hybrida* did not increase significantly under NLP, possibly because the night-time light intensity was too weak to cause a significant change in the content of sugars and starch. Some studies point out that sugars, such as disaccharides, raffinose family oligosaccharides and fructans, can act as antioxidants, which might function as signals affecting the production of ROS, and can also act as true ROS scavengers to protect chloroplasts and stabilize photosynthesis under stress conditions (Keunen et al. 2013). Future studies should further explore the responses and effects of different sugar species under NLP. It is worth noting that considering the diurnal variation in sugars and starch, the time of day for measuring carbohydrates is crucial in researching the influences of continuous light on leaf carbohydrate metabolism (Haque et al. 2015). We look forward to more research to explore how carbohydrates change at different times of day under NLP.

A unifying hypothesis of the effects of continuous light on plants has not yet been presented. Experiments in horticultural systems and few urban plants have shown that plant photosynthesis or biomass responses to artificial stimuli can be positive, negative or neutral (Haque et al. 2017, 2015; Min and Sherman 2010; van Gestel et al. 2005; Velez-Ramirez et al. 2011; Zhang et al. 2020). The reduction in the photosynthetic rate in our study under NLP supported these studies, which confirmed that continuous light can disturb the circadian rhythm and cause negative effects, including excessive accumulation of ROS and reduced photosynthetic rate, efficiency of the electron transport chain and maximum photochemical quantum yield in plants (Kwak et al. 2018; Meravi and Prajapati 2020; van Gestel et al. 2005; Zhang et al. 2020). Currently, the duration and intensity of light required to disrupt circadian rhythms under field conditions are unknown (Gaston et al. 2013). Furthermore, some studies point out that diurnal temperature variations can reset the circadian rhythms and alleviate or eliminate continuous light-induced negative effects in some species, but the physiological mechanisms behind these effects are less clear (Haque et al. 2015; Ikkonen et al. 2015; Velez-Ramirez et al. 2011). It should be noted that although the shadows generated by the device did not obscure the selected leaves and plants during the measurement period in August, the shadow may briefly block the leaves or plants in the plot in June, and whether this possible brief shade affects our results should be further explored in the future research. Overall, the effects of NLP on plants vary with light intensity, spectral distribution, plant species and other environmental

factors. Estimating and regulating the effects of NLP on urban plants is a requirement to maintain the health of urban ecosystems. As the use of artificial light at night is increasing at a continuous and dramatic step (Falchi et al. 2016; Levy et al. 2020), urban plants will suffer more stresses from NLP. Considering that the spectral distribution of night-time light in cities has great heterogeneity and that its effect varies with plant species, planting urban tree species with NLP tolerance and installing appropriate light sources are very important and should be based on further studies on the physiological response and adaptation of urban trees.

Conclusions

The present study deepens our understanding of the biochemical mechanisms underpinning the deleterious impacts of NLP on urban plants. Our findings showed that NLP caused photoinhibition and oxidative stress, which can reduce the pigment contents, lower the values of L_s , Φ_{PSII} , ETR and qp , and increase the MDA and TAC contents, leading to a decrease in P_n . However, those deleterious effects were related to the spectral distribution of artificial light sources and species. Indeed, both *E. japonicus* and *R. hybrida* experienced more severe oxidative stress conditions and had more pronounced effects on photosynthesis and physiological characteristics under blue and red light, and no significant difference was found between the Blue and Red treatments. Furthermore, green light had no significant effect on either species, and the effect of white light only occurred on *E. japonicus* and not on *R. hybrida*. Sugars and starch in the leaves of *E. japonicus* and *R. hybrida* did not change significantly under NLP, possibly because the NLP intensity was too weak to cause a significant change in the contents of sugars and starch. At the same time, we also found that the G_s of *E. japonicus* decreased under the Blue and Red treatments, which may be due to the continuous blue and red light destroying the function of the stomata and reducing the stomatal area. Considering that the spectral distribution of artificial light at night in cities has great heterogeneity, and that its effect varies with plant species, it is important to arrange tree species with NLP tolerance and install appropriate light sources in urban areas based on the corresponding physiological responses and adaptation of urban trees.

Abbreviations

NLP	Night-time light pollution
Chla	Chlorophyll a
Chlb	Chlorophyll b
Chla + b	Chlorophyll a + b
Chla/b	Chlorophyll a/b

P_n	Net photosynthetic rate
L_s	Stomatal limit value
G_s	Stomatal conductance
Φ_{PSII}	Effective quantum yield
ETR	Apparent electron transfer rate
qp	Photochemical quenching coefficient
MDA	Malondialdehyde
TAC	Total antioxidant capacity
NCSs	Nonstructural carbohydrates

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-023-00449-6>.

Additional file 1: Figure S1. Wave length distributions irradiated by green (a), white (b), blue (c), and red (d) LEDs. **Figure S2.** Images of the field experiment at dawn (a) and night (b).

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Author contributions

DH: method, writing—review; YW: writing—original draft, implement experiment; ZL: implement experiment; JZ: implement experiment.

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Data availability

Data can be made available on request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no conflict of interest.

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