



## Research Article



# Optimizing the Light Environment for the Cultivation of Ornamental Tree Species: the Influence of LED Spectra on the Photosynthetic Apparatus and Secondary Metabolism

Nataliia Zaimenko, Nataliia Didyk\*, Alla Liubinska

M.M. Gryshko National Botanical Garden of the National Academy of Sciences of Ukraine, Kyiv, Ukraine

ID Nataliia Zaimenko: <https://orcid.org/0000-0003-2379-1223>ID Nataliia Didyk: <https://orcid.org/0000-0001-8448-7490>ID Alla Liubinska: <https://orcid.org/0000-0002-1873-8252>

## Article Details:

Received: 2026-02-22

Accepted: 2026-05-05

Available online: 2026-05-31

DOI: <https://doi.org/10.15414/ainhql.2026.0005>

In urban environments, green areas often lack sunlight during the day and rely on artificial illumination at night, which reduces their ecological services. Application of LED illumination with specific spectral characteristics in green areas of megacities could enhance their aesthetic value and safety and optimize the health of urban vegetation. The effects of monochrome red, blue, and mixed red-blue LED lighting on photosynthetic pigments, flavonoids, anthocyanins, and tannin accumulation in the leaves of the shaded seedlings of ornamental woods *Pinus sylvestris* L., *Rhododendron catawbiense* Michx., *Magnolia × soulangeana* Soul.-Bod., *Magnolia Kobus* DC., and *Ginkgo biloba* L. were studied in pot experiments. The species specificity of physiological responses to LED illumination with a specific spectral composition was established. The contents of photosynthetic pigments and tannins in the leaves of the heliophytes *M. × soulangeana*, *M. kobus*, *G. biloba*, and *P. sylvestris* were the most effectively stimulated by monochrome red LED lighting. While the accumulation of flavonoids in the leaves of the mentioned test-plants was the highest at red-blue or monochrome blue LED lighting. In the shade-tolerant *Rh. catawbiense* the different tendency was observed: the highest levels of photosynthetic pigments in the leaves were observed in the plants treated with red-blue LED lighting, the highest content of flavonoids was observed in plants treated with monochrome red. The monochrome blue LED lighting had the highest promoting effect on anthocyanin synthesis in all test-plants. Thus, using five ornamental tree species with different light requirements, it was demonstrated that supplemental red and blue LED lighting could effectively optimize photosynthesis and secondary metabolism in urban woody vegetation exposed to light deficiency.

**Keywords:** woody ornamentals, LED spectra, photosynthetic pigments, secondary metabolites

\*Corresponding Author: Nataliia Didyk, M.M. Gryshko National Botanical Garden of the National Academy of Sciences of Ukraine, Sadovo-Botanichna str. 1, 01103 Kyiv  
✉ [nataliya\\_didyk@ukr.net](mailto:nataliya_didyk@ukr.net)

## Introduction

Light provides energy for photosynthesis and regulates plant growth, development, phenological changes, and secondary metabolism. For photosynthesis, the most important spectral range of wavelengths called PAR (photosynthetically active radiation) is from 400 to 750 nm (Zhen and Bugbee, 2020). Ultraviolet radiation (280–400 nm), although not included in the PAR range, has a significant effect on plant development and biochemical features (Li and Kubota, 2009).

Urban vegetation is suffering from inadequate light quality due to shading by buildings, scattering of sunlight by smog particles, as well as by nighttime artificial light pollution. These conditions could disrupt basic physiological processes such as photosynthesis, respiration, leaf and reproductive organ morphogenesis, photoperiodic reactions, and phenological phases (Petrushkevych and Korshykov, 2020). This is driving researchers to look for ways to improve urban lighting conditions, taking into account the needs of plant species used for landscaping.

The positive effect of the LED illumination on the vitality of plants exposed to low natural sunlight has been confirmed by many studies (Li et al., 2016; Talib et al., 2020; Qiao et al., 2025; Zhang et al., 2025). It was also found that the negative impact of nighttime lighting can be significantly minimized by regulating its spectral composition (Friulla and Varone, 2025). Despite this, only limited studies have examined the physiological and molecular mechanisms underlying these phenomena (Sena et al., 2024). In addition, the majority of works focus on the processes related to photosynthetic productivity, food and medicinal value of the test-plants, while the influence of the LED illumination on signaling pathways and defense mechanism have been given little attention (Li and Kubota, 2009; Trivellini et al., 2023; Sena et al., 2024). The available information on the effects of LED spectra on the secondary metabolism of higher plants is insufficient and contradictory (Sena et al., 2024). The lack of such knowledge limits the application of LED technologies in the urban out-door and in-door greening, vertical farming etc. On the other hand, it is known that the use of artificial light in cities is increasing by 6% annually, with LED lamps replacing HPS lamps due to their greater environmental safety and lower operating costs (Friulla and Varone, 2025). This provides additional opportunities to optimize the vital state of urban vegetation through appropriate LED spectral design.

Plants possess an array of photoreceptors, such as and phytochromes, cryptochromes (CRYs), UVRESISTANCE LOCUS8 (UVR8), and phototropins (PHOTs), which are activated by a certain light spectrum and regulate growth reactions as well as phytochemical profiles (Wei et al., 2023; Zhu et al., 2025). CRYs regulate photomorphogenesis, photoperiodic flowering, and circadian rhythm (Wei et al., 2023). PHOTs are mediating phototropism, chloroplast movement, stomatal opening, and leaf expansion (Wei et al., 2023). Phytochromes regulate the synthesis of photosynthetic pigments, growth and development, including the induction of seed germination, seedling de-etiolation, flowering time, fruit quality, root elongation, and tolerance to biotic and abiotic stressors (Demotes-Mainard et al., 2016; Wei et al., 2023).

The effects of LED lamps with different spectral characteristics on the performance of higher plants is actively discussed in the scientific literature. The most studied in this regard are red (600–700 nm) and blue (400–500 nm) spectral LED lamps, which are recognized as the most effective in stimulating photosynthesis, growth, and development, as well as the synthesis of protective antioxidants (Wei et al., 2023; Zhu et al., 2025). In recent years, the focus has shifted to other parts of the spectrum, in particular, more attention is being paid to far-red (700 to 750 nm) illumination (Zhen and Bugbee, 2020). The role of green (500–600 nm) and ultraviolet (280–400 nm) lighting is also being reconsidered (Li and Kubota, 2009; Smith et al., 2017; Lee et al., 2021). In particular, ultraviolet radiation (280–400 nm) has a significant effect on plant morphology and biochemistry. In moderate doses, it can stimulate the synthesis of carotenoids, flavonoids, anthocyanins, and other phenolic secondary metabolites that perform protective functions in plants. However, excessive UV-light can damage DNA and inhibit photosynthesis (Li and Kubota, 2009; Lee et al., 2021).

Numerous experimental data indicate that each plant species has its own unique requirements for the spectral composition of light (Hew et al., 2024). For example, blue light has been shown to enhance phenolic biosynthesis in *Matricaria chamomilla* (Maham et al., 2025), phenolic and flavonoid concentrations in *Ocimum basilicum* (Jokic et al., 2025), amino acids, organic acids, fatty acids, and flavonoid glycosides in *Oryza sativa* (Jung et al., 2013). While red light favors flavonoids in *Matricaria chamomilla* (Maham et al., 2025), accumulation of rosmarinic acid in *Anethum graveolens* (Goswami et al., 2023); accumulation of carbohydrates in *Kaempferia parviflora* (Wei et al.,

2024). The mechanisms underlying these species specificity of plant responses to light spectra are still unexplored. Primary and secondary metabolic reactions to the light treatments also differ, with each phytochemical being stimulated by a specific light spectrum (Alrajhi et al., 2023).

Despite contemporary advances in studying the effects of LED spectra on physiological processes in plants, no comprehensive understanding has been achieved of how LED spectra regulate secondary metabolism and other processes involved in adaptation to environmental stresses. Knowledge gaps remain regarding species-specific responses to different light spectra. Elucidation of the aforementioned aspects will be instrumental in selecting resilient ornamentals for urban conditions and in optimizing green spaces in smart city planning.

The objective of our study was to evaluate the effect of different LED spectra on the photosynthetic pigments and secondary metabolism of five ornamental woody species (*Pinus sylvestris*, *Rhododendron catawbiense*, *Magnolia × soulangeana*, *Magnolia kobus*, *Ginkgo biloba*), which are gaining popularity in modern green landscaping in Ukraine and other European countries.

## Material and Methodology

### Plant material and experimental design

Three-year-old seedlings of ornamental woody species *Pinus sylvestris*, *Rhododendron catawbiense*, *Magnolia × soulangeana*, *Magnolia kobus*, and *Ginkgo biloba*, grown in the nursery greenhouse of the M.M. Gryshko National Botanical Garden of the National Academy of Sciences of Ukraine (Kyiv), were used in the study.

Forty uniform seedlings of each species were divided into four groups (10 plants per group) and placed in Plexiglas growth chambers (2 × 1.5 × 1.5 m) equipped with LED lighting. The following light treatments were applied (Table 1):

1. direct sunlight;

2. shading (chambers covered with a 4 mm polyvinyl chloride (PVC) sheet);
3. shading + blue LED;
4. shading + red LED;
5. shading + combined red and blue LED (4 : 1).

Light intensity was measured using an LI-250A light meter (LI-COR, USA) equipped with a PAR sensor. Plants were grown at 24–26 °C and 60–70% soil moisture (of total field capacity) for 21 days. The experiment was conducted in four replicates.

### Sample preparation

Leaves and needles were randomly collected from the middle part of the seedlings and cut into small pieces. Fresh material was used to determine the content of photosynthetic pigments, flavonoids, and anthocyanins. For tannin analysis, leaves were air-dried in the shade at room temperature to constant weight.

### Determination of photosynthetic pigments

The content of photosynthetic pigments (chlorophylls and carotenoids) was extracted with DMCO (dimethyl sulfoxide) for 4 hours in a thermostat at a temperature of 70 °C (Hiscox and Israelstam, 1979). Quantitative content was determined according to Wellburn (1994) using a spectrophotometer SPECORD 200 (Analytik Jena). Measurements were performed at wavelengths of 644 nm (chlorophyll *b*), 662 nm (chlorophyll *a*), and 440 nm (carotenoids).

### Determination of flavonoids

Flavonoids were extracted with 70% ethanol from freshly harvested and crushed leaves for 24 hours in a refrigerator. The quantitative content of flavonoids was determined using a qualitative reaction with a 2% AlCl<sub>3</sub> solution in 98% ethanol at a wavelength of 410 nm with a spectrophotometer (SPECORD 200, Analytik Jena), using quercetin as a standard (Pavliuchenko et al., 2021).

**Table 1** Description of lighting treatments

Lighting type	Wavelength (nm)	Luminous flux (μmol·m <sup>-2</sup> ·s <sup>-1</sup> )	Lamp model
Direct sunlight	380–780	1,000–2,000	absent
Shading	380–780	50–100	absent
Red-blue (4 : 1) LED lamp	640–660 450–500	192	T8-2835-1,2 FRB Ledmax
Red LED lamp	640–660	122	T8SL-08R G13 Ledmax
Blue LED lamp	450–500	122	T8SL088G13 Ledmax

### Determination of anthocyanins

Anthocyanins were extracted with 96% ethyl alcohol with 1% hydrochloric acid from freshly harvested and crushed leaves. The quantitative content was determined at a wavelength of 546 nm using a spectrophotometer SPECORD 200 (Analytik Jena) (Pavliuchenko et al., 2021).

### Determination of tannins

Air-died foliar samples were extracted with boiling distilled water, and then infused in a water bath for an hour. The quantitative content was determined by titration with 0.1% potassium permanganate solution of a mixture of the filtered extract with indigo carmine (Mardar and Serdyuk 2008).

### Statistical analysis

Data were analyzed using parametric statistical methods at a 95% confidence level. Results are presented as mean ± standard error (SE). Differences between treatments were evaluated using one-way ANOVA followed by Tukey’s post hoc test at  $p < 0.05$ .

### Results and Discussion

The type of lighting significantly affected the content and ratio of photosynthetic pigments in the leaves or needles of the studied test-plants (Table 2). Shading caused a significant decrease in the content of chlorophyll *a*, the ratios of chlorophyll *a/b* and chlorophyll *a + b*/carotenoids. At the same time, the content of chlorophyll *b* and carotenoids increased,

**Table 2.** The effect of lighting spectral characteristics on the content of photosynthetic pigments in the leaves or needles of woody ornamentals

Testplant	Photosynthetic pigments	Shading				
		Direct sunlight	control	red	blue	red-blue (4 : 1)
<i>Magnolia × soulangeana</i>	chlorophyll <i>a</i>	2.28 ± 0.09 <sup>a</sup>	1.79 ± 0.10 <sup>b</sup>	1.88 ± 0.07 <sup>ab</sup>	0.39 ± 0.06 <sup>c</sup>	1.37 ± 0.08 <sup>d</sup>
	chlorophyll <i>b</i>	0.61 ± 0.04 <sup>a</sup>	0.83 ± 0.02 <sup>b</sup>	0.87 ± 0.04 <sup>b</sup>	0.13 ± 0.03 <sup>c</sup>	0.31 ± 0.03 <sup>c</sup>
	carotenoids	0.24 ± 0.01 <sup>a</sup>	0.37 ± 0.02 <sup>b</sup>	0.39 ± 0.02 <sup>b</sup>	0.06 ± 0.01 <sup>c</sup>	0.19 ± 0.02 <sup>a</sup>
	chl <i>a</i> /chl <i>b</i>	3.71	2.15	2.15	3.01	4.39
	(chl <i>a</i> +chl <i>b</i> )/carotenoids	12.05	7.05	7.05	8.6	8.89
<i>Magnolia kobus</i>	chlorophyll <i>a</i>	2.45 ± 0.11 <sup>a</sup>	2.2 ± 0.08 <sup>a</sup>	2.35 ± 0.05 <sup>a</sup>	0.74 ± 0.10 <sup>b</sup>	1.11 ± 0.04 <sup>b</sup>
	chlorophyll <i>b</i>	1.22 ± 0.03 <sup>a</sup>	1.23 ± 0.02 <sup>a</sup>	1.31 ± 0.02 <sup>a</sup>	0.39 ± 0.02 <sup>b</sup>	0.48 ± 0.03 <sup>b</sup>
	carotenoids	0.46 ± 0.02 <sup>a</sup>	0.47 ± 0.01 <sup>a</sup>	0.5 ± 0.01 <sup>a</sup>	0.2 ± 0.02 <sup>b</sup>	0.25 ± 0.01 <sup>b</sup>
	chl <i>a</i> /chl <i>b</i>	2.01	1.79	1.79	1.88	2.31
	(chl <i>a</i> +chl <i>b</i> )/carotenoids	8.01	7.32	7.32	5.71	6.34
<i>Rhododendron catawbiense</i>	chlorophyll <i>a</i>	2.08 ± 0.12 <sup>a</sup>	1.02 ± 0.13 <sup>b</sup>	2.04 ± 0.11 <sup>a</sup>	2.16 ± 0.10 <sup>a</sup>	3.59 ± 0.11 <sup>c</sup>
	chlorophyll <i>b</i>	0.47 ± 0.03 <sup>a</sup>	0.5 ± 0.04 <sup>a</sup>	0.46 ± 0.05 <sup>a</sup>	0.48 ± 0.04 <sup>a</sup>	0.68 ± 0.02 <sup>b</sup>
	carotenoids	0.24 ± 0.02 <sup>a</sup>	0.25 ± 0.02 <sup>a</sup>	0.24 ± 0.02 <sup>a</sup>	0.26 ± 0.01 <sup>a</sup>	0.39 ± 0.02 <sup>b</sup>
	chl <i>a</i> /chl <i>b</i>	4.44	2.05	4.44	4.53	5.29
	(chl <i>a</i> +chl <i>b</i> )/carotenoids	10.49	6.12	10.49	10.06	10.87
<i>Ginkgo biloba</i>	chlorophyll <i>a</i>	2.27 ± 0.15 <sup>a</sup>	1.28 ± 0.12 <sup>b</sup>	3.23 ± 0.13 <sup>c</sup>	2.43 ± 0.13 <sup>a</sup>	2.72 ± 0.15 <sup>a</sup>
	chlorophyll <i>b</i>	0.49 ± 0.04 <sup>a</sup>	0.51 ± 0.05 <sup>a</sup>	0.7 ± 0.04 <sup>b</sup>	0.45 ± 0.04 <sup>a</sup>	0.55 ± 0.03 <sup>a</sup>
	carotenoids	0.22 ± 0.02 <sup>a</sup>	0.24 ± 0.01 <sup>a</sup>	0.31 ± 0.01 <sup>b</sup>	0.21 ± 0.02 <sup>a</sup>	0.24 ± 0.01 <sup>a</sup>
	chl <i>a</i> /chl <i>b</i>	4.61	2.52	4.61	5.42	4.91
	(chl <i>a</i> +chl <i>b</i> )/carotenoids	12.58	7.62	12.58	13.65	13.52
<i>Pinus sylvestris</i>	chlorophyll <i>a</i>	1.33 ± 0.09 <sup>a</sup>	0.78 ± 0.10 <sup>b</sup>	1.9 ± 0.09 <sup>c</sup>	1.14 ± 0.11 <sup>a</sup>	1.46 ± 0.08 <sup>a</sup>
	chlorophyll <i>b</i>	0.37 ± 0.03 <sup>a</sup>	0.38 ± 0.02 <sup>a</sup>	0.44 ± 0.02 <sup>a</sup>	0.31 ± 0.02 <sup>a</sup>	0.23 ± 0.03 <sup>b</sup>
	carotenoids	0.21 ± 0.01 <sup>a</sup>	0.28 ± 0.01 <sup>b</sup>	0.32 ± 0.01 <sup>b</sup>	0.19 ± 0.01 <sup>a</sup>	0.2 ± 0.01 <sup>a</sup>
	chl <i>a</i> /chl <i>b</i>	3.61	2.05	4.31	3.66	6.41
	(chl <i>a</i> +chl <i>b</i> )/carotenoids	8.24	4.17	7.26	7.69	8.63

Notes: mean ± standard error; different letters indicate values, which reliably differed from one another within one line of the table according to the results of comparison using the Tukey test

a typical response of the photosynthetic system to shading (Mohd Yusof et al., 2021).

Monochrome red LED light stimulated the synthesis of photosynthetic pigments (chlorophylls *a*, *b*, and carotenoids) in the leaves of all investigated woody plant seedlings (Table 2). Red light spectrum is known to be best absorbed by chlorophyll *a* and *b*, providing energy for photosynthesis. The predominance of this spectrum is a signal of exposure to sunlight and activates phytochromes, which trigger the expression of genes responsible for chloroplast development (Trivellini et al., 2023).

Monochrome blue LED light stimulated the synthesis of chlorophylls *a* and *b* to a lesser extent than red in the leaves of heliophytes *G. biloba* and *P. sylvestris* and inhibited chlorophyll *a*, chlorophyll *b*, and carotenoids accumulation in the leaves of *M. × soulangeana* and *Magnolia kobus*. While for the shade-tolerant *Rh. catawbiense*, blue LED light had the maximum promoting effect on foliar photosynthetic pigments.

The combination of red and blue (4 : 1) LED lighting significantly reduced the negative effect of blue lighting on the content of photosynthetic pigments in the leaves of *M. kobus* and *M. × soulangeana* and synergistically enhanced the stimulating effect of monochrome LED light on the content of photosynthetic pigments in the leaves of *Rh. catawbiense*. This type of lighting also enhanced the chl *a/b* ratio in the leaves of all test-plants to the greatest extent. This indicated the induction of light-acclimation processes from the “shadow” to the “light” phenotype in the studied ornamental seedlings under additional red-blue LED illumination. The relative

increase in the number of reaction centers (chl *a*) leads to an increase in assimilation and growth. At the same time, a certain species-specificity of morphogenetic changes in response to additional red-blue lighting was observed. In particular, in *M. kobus*, *Rh. catawbiense* and *G. biloba*, the leaf blade area increased (Figure 1, A–C), while in *M. × soulangeana*, the leaf blade area slightly decreased. In *P. sylvestris*, red-blue LED lighting increased the thickness and stiffness of the needles, although their length was lower (Figure 1 D).

The application of LED lighting increased the ratio (chl *a* + chl *b*)/carotenoids, indicating improved seedling health and mitigation of light stress. The red-blue LED spectrum most effectively reduced this ratio in *M. × soulangeana*, *P. sylvestris*, and *Rh. catawbiense*. While monochrome red and blue LED light spectra demonstrated the highest effectiveness in increasing this ratio in *M. kobus*, *G. biloba*, respectively. Carotenoids are auxiliary pigments of the photosynthetic apparatus that expand the absorption spectrum of chlorophylls in the blue region of the spectrum (380–450 nm) and transfer the energy of the excited state to chlorophyll. Carotenoids also protect chlorophyll from photooxidation and destruction by oxygen radicals (Hashimoto et al., 2015). Shaded tree seedlings, due to additional illumination with red, blue, and red-blue light, used energy more efficiently for photosynthesis, rather than for self-protection. This confirms that the selected LED lamp intensity is comfortable and productive for the studied tree seedlings. Our results confirm the high efficacy of red-blue lighting in stimulating of photosynthetic function (Park and Runkle, 2018).



**Figure 1** The effect of red-blue LED light on the size and color of leaves of *Magnolia kobus* (A), *Magnolia × soulangeana* (B); *Ginkgo biloba* (C) and needles of *Pinus sylvestris* (D)  
1 – shading without LED lighting, 2 – shading with the red-blue LED lighting

The positive effect of supplementary red and blue LED lighting on the photosynthesis, growth, and development of various plant species exposed to sunlight deficient conditions, such as a greenhouse during winter periods or the vertical multi-tier hydroponic system, was demonstrated by other authors (Li et al., 2016; Naznin et al., 2019; Talib et al., 2020; Malabadi et al., 2024; Qiao et al., 2025). Comparison of the results of different authors show that supplementary red LED light was efficient in stimulating leaf area, stem length, biomass, root indices, foliar chlorophyll content, net photosynthesis rate, quantum yield of PSII, electron transfer rate (Li et al., 2016; Talib et al., 2020; Qiao et al., 2025). Supplementary blue LED lighting was beneficial to the test-plant's stem diameter, leaf thickness, and antioxidant capacity (Lu et al., 2012; Li et al., 2016; Hooks et al., 2022). In our research, a similar trend was observed for heliophytic woody ornamentals growing in shaded conditions. While the shade tolerant *Rh. catawbiense* demonstrated the maximum growth and photosynthetic activity when exposed to combined red and blue supplemental LED lighting.

Shading of seedlings of woody ornamentals significantly suppressed the accumulation of the total flavonoids, although it stimulated the synthesis of anthocyanins in the leaves of test plants (Tables 3–4). Light intensity

is recognized as a key factor regulating flavonoid synthesis, especially in heliophytes (Idris et al., 2018; Qin et al., 2024; Zhu et al., 2025). It is established that light quality and photoperiods can indirectly regulate the expression of flavonoid-regulated genes and thus control flavonoid accumulation through modulation of cryptochromes (Jaakola, 2013). Some heliophytes like *Ginkgo biloba* and *Erigeron breviscapus*, demonstrate linear positive correlation of flavonoid accumulation with light intensity (Idris et al., 2018). While others, such as *Lithocarpus litseifolius* (Hance) Chun. (Fagaceae), and *Piper aduncum* L. produce maximum flavonoids at about 40 and 50% shading, respectively, and fewer flavonoids at higher shading or 100% irradiance (Idris et al., 2018).

Anthocyanins are plant secondary metabolites belonging to the flavonoid family and are characterized by high antioxidant capacity, as they contain multiple phenol hydroxyl groups that are strong hydrogen and electron donors (Li and Ahammed, 2023). In various plant species, the intensification of free radical reactions under light deficiency promotes the transcription of anthocyanin-related genes and, ultimately, anthocyanin synthesis, thereby contributing to plant adaptation to stress conditions (Guo et al., 2022; Shen et al., 2023; Zhu et al., 2025).

**Table 3** The effect of LED lighting with different spectral characteristics on the total content of flavonoids (mg·g<sup>-1</sup> FW) in the leaves of the woody ornamental seedlings

Lighting conditions	<i>Magnolia × soulangeana</i>	<i>Magnolia kobus</i>	<i>Rhododendron catawbiense</i>	<i>Ginkgo biloba</i>	<i>Pinus sylvestris</i>
Direct sunlight	14.4 ± 0.2 <sup>a</sup>	15.6 ± 0.1 <sup>a</sup>	14.5 ± 0.2 <sup>a</sup>	14.1 ± 0.2 <sup>a</sup>	6.0 ± 0.1 <sup>a</sup>
Shading	11.1 ± 0.2 <sup>b</sup>	9.4 ± 0.1 <sup>b</sup>	10.0 ± 0.1 <sup>b</sup>	8.5 ± 0.2 <sup>b</sup>	4.7 ± 0.2 <sup>b</sup>
Shading+ red LED	3.0 ± 0.1 <sup>c</sup>	4.6 ± 0.2 <sup>c</sup>	26.1 ± 0.2 <sup>c</sup>	10.5 ± 0.1 <sup>c</sup>	2.4 ± 0.2 <sup>c</sup>
Shading+ blue LED	4.6 ± 0.1 <sup>c</sup>	5.3 ± 0.2 <sup>c</sup>	19.9 ± 0.2 <sup>d</sup>	9.3 ± 0.2 <sup>b</sup>	2.7 ± 0.2 <sup>c</sup>
Shading+ red and blue LED	9.46 ± 0.3 <sup>b</sup>	7.26 ± 0.2 <sup>d</sup>	15.56 ± 0.1 <sup>a</sup>	8.66 ± 0.2 <sup>b</sup>	2.7 ± 0.1 <sup>c</sup>

Notes: Different letters indicate values, which reliably differed from one another within one line of the table according to the results of comparison using the Tukey test

**Table 4** The effect of LED lighting with different spectral characteristics on the content of anthocyanins (mg·kg<sup>-1</sup> FW) in the leaves of seedlings of woody ornamentals

Lighting conditions	<i>Magnolia × soulangeana</i>	<i>Magnolia kobus</i>	<i>Rhododendron catawbiense</i>	<i>Ginkgo biloba</i>	<i>Pinus sylvestris</i>
Direct sunlight	0.16 ± 0.03 <sup>a</sup>	0.13 ± 0.03 <sup>a</sup>	0.81 ± 0.04 <sup>a</sup>	n. <sup>d</sup> .	n. <sup>d</sup> .
Shading	0.22 ± 0.03 <sup>a</sup>	0.84 ± 0.02 <sup>b</sup>	1.14 ± 0.05 <sup>b</sup>	0.07 ± 0.03 <sup>a</sup>	0.10 ± 0.03 <sup>a</sup>
Shading+ red LED	0.18 ± 0.02 <sup>a</sup>	0.42 ± 0.03 <sup>c</sup>	0.42 ± 0.03 <sup>c</sup>	n. <sup>d</sup> .	0.12 ± 0.03 <sup>a</sup>
Shading+ blue LED	1.54 ± 0.01 <sup>b</sup>	1.13 ± 0.03 <sup>d</sup>	1.86 ± 0.03 <sup>d</sup>	0.14 ± 0.03 <sup>a</sup>	0.45 ± 0.03 <sup>b</sup>
Shading+ red and blue LED	1.11 ± 0.02 <sup>b</sup>	1.04 ± 0.02 <sup>d</sup>	0.44 ± 0.04 <sup>c</sup>	n. <sup>d</sup> .	0.13 ± 0.03 <sup>a</sup>

Notes: Different letters indicate values, which reliably differed from one another within one line of the table according to the results of comparison using the Tukey test; \*n.d. means not detected by the method used

The application of LED lighting significantly affected the synthesis of these secondary metabolites. At the same time, a significant dependence was observed on both the LED spectral characteristics and the test plant species. For example, monochrome red and blue LED light stimulated flavonoid synthesis in the leaves of *Rh. catawbiense* and *G. biloba*, but significantly suppressed this process in *M. kobus*, *M. × soulangeana*, and *P. sylvestris*. Combining the blue and the red spectra mitigated the negative effect of the latter on the flavonoid content in the magnolia leaves and pine needles, but also reduced the stimulating effect of monochrome lighting on the synthesis of flavonoids in the leaves of *Rh. catawbiense* and *G. biloba*.

Flavonoids perform multiple functions in plants, such as protection from abiotic and biotic stresses (i.e. UV-radiation, drought, toxic metals, phytopathogens), signaling, regulators of growth and development, allelochemicals, detoxifying agents and pollinator attractants (Idris et al., 2018). A decrease in their content at shading indicates a decrease in the general adaptive capacity of the test-plants. By manipulating the intensity and spectral composition of supplemental LED lighting, it is possible to significantly optimize the synthesis of these secondary metabolites in plants. In particular, Orlando et al. (2022) showed that the total flavonoid content in *Crocus sativus* L. tepals was significantly enhanced under supplemental LED lighting comprising 50% red, 18% green, and 38% blue. Blue light, via the cryptochromes and phototropins, was proven to drive the synthesis of total phenolics and flavonoids in *Lactuca sativa* L., *Ocimum basilicum* L., *Lycopersicon esculentum* Mill. and anthocyanins in *Fragaria × ananassa* Duchesne (Paradiso, & Proietti, 2022). The supplemental white and red-blue spectrum increased total flavonoids and other polyphenols synthesis in *Curcuma longa* L. (Marchant et al., 2022). Supplemental red and blue light treatments increased, antioxidant capacity and

concentrations of anthocyanins, carotenoids, and total phenolics in *Lactuca sativa* cv. 'Red Mist' (Hooks et al., 2022). Zhu et al. (2025) studied the effects of various light spectra, ranging from ultraviolet-B to red, on the accumulation of anthocyanins and other phenolics in *Lactuca sativa* cv. Red Salad Bowl and Rouxai. and found that low-intensity UVB light was the most effective at promoting anthocyanins and total phenolics synthesis, followed by blue light. In another study on red leaf lettuce, it was shown that anthocyanin content increased with increasing the blue-to-red ratio in the light spectra (Shoji et al., 2010).

In our study, the most effective in stimulating anthocyanin synthesis in the leaves of the tested woody ornamentals was monochrome blue LED light. While a monochrome red LED light, as a rule, reduced the content of anthocyanins in the leaves of angiosperm seedlings. The combination of red and blue spectra significantly stimulated anthocyanin synthesis in the leaves of *M. × soulangeana* and *M. kobus*, but reduced this indicator in *Rh. catawbiense*. A similar trend was found by other authors who studied the effects of monochrome red and blue LED light on other plant species.

Shading suppressed the synthesis of tannins in the leaves of heliophytes *M. × soulangeana*, *M. kobus*, *G. biloba*, and *P. sylvestris* (Table 5). While in the shade-tolerant *Rh. catawbiense*, the content of tannins in the leaves of the shaded test-plants exceeded this parameter observed in plants growing under direct sunlight. A similar tendency was observed by other authors, investigating the effect of the light intensity on tannin accumulation in plants. In particular, it was shown that shading negatively affected the concentration of condensed tannins in the leaves of ericaceous grasses (Hofland-Zijlstra and Berendse et al., 2009), *Lotus corniculatus* (Arcioni et al., 2005), *Larix gmelinii* (Yan et al., 2014). Several distinct

**Table 5** Effect of LED lighting with different spectral characteristics on the content of tannins (mg·kg<sup>-1</sup> DW) in the leaves of woody ornamentals

Lighting conditions	<i>Magnolia × soulangeana</i>	<i>Magnolia kobus</i>	<i>Rhododendron catawbiense</i>	<i>Ginkgo biloba</i>	<i>Pinus sylvestris</i>
Direct sunlight	26.1 ± 0.1 <sup>a</sup>	17.0 ± 0.2 <sup>a</sup>	25.3 ± 0.03 <sup>a</sup>	10.4 ± 0.2 <sup>a</sup>	5.4 ± 0.2 <sup>a</sup>
Shading	13.9 ± 0.3 <sup>b</sup>	12.1 ± 0.2 <sup>b</sup>	28.3 ± 0.2 <sup>b</sup>	8.8 ± 0.1 <sup>b</sup>	5.1 ± 0.2 <sup>a</sup>
Shading+ red LED	28.4 ± 0.2 <sup>a</sup>	30.6 ± 0.2 <sup>c</sup>	15.9 ± 0.1 <sup>c</sup>	9.9 ± 0.2 <sup>a</sup>	10.4 ± 0.3 <sup>b</sup>
Shading+ blue LED	9.6 ± 0.1 <sup>c</sup>	7.9 ± 0.2 <sup>d</sup>	11.9 ± 0.3 <sup>d</sup>	5.3 ± 0.2 <sup>c</sup>	5.7 ± 0.1 <sup>a</sup>
Shading+ red and blue LED	29.8 ± 0.2 <sup>a</sup>	31.0 ± 0.1 <sup>c</sup>	27.6 ± 0.1 <sup>b</sup>	9.4 ± 0.3 <sup>a</sup>	10.3 ± 0.3 <sup>b</sup>

Notes: Different letters indicate values, which reliably differed from one another within one line of the table according to the results of comparison using the Tukey test

mechanisms of tannin biosynthesis were revealed, one of which found in the above-ground organs is light quality-mediated (Hassanpour et al., 2011).

Application of LED lighting significantly affected the intensity of tannin synthesis in the leaves of the studied test plants. At the same time, red and red-blue LED light stimulated the synthesis of tannins in the leaves of heliophytes, while for the shade-tolerant *Rh. catawbiense* the opposite trend was observed. The synthesis of tannins in the leaves of *M. × soulangeana*, *M. kobus* and *P. sylvestris* was most effectively stimulated by red-blue LED light, and in the leaves of *G. biloba* by monochrome red LED light.

The positive effect of supplemental red and blue LED lighting on tannin biosynthesis has been demonstrated in a number of studies. In particular, Marchant et al. (2022) demonstrated that supplemental white and red-blue LED lighting significantly increased total tannin content in *Curcuma longa*. Benincasa et al. (2020) found an increase in tannin contents in *Triticum monococcum* L. by blue LED lighting. In *Triticum turgidum* L., red LED lighting increased the total content of tannins and flavonoids. Nowruzi et al. (2025) revealed that supplemental red and blue light increased total phenolics, flavonoids, and tannins in *Fischerella* sp, with red light having the greatest effect.

Tannins are well-known protective secondary metabolites, involved in plant tolerance to abiotic and biotic stressors due to their high potential antioxidant effects (Yan et al., 2014; Iqbal, and Poór 2025). Therefore, stimulation of the accumulation of these compounds in the leaves of seedlings by red and red-blue LED lighting indicates an increase in the systemic resistance of the studied woody ornamentals (Iqbal and Poór 2025). This is especially relevant for plants at risk of damage from phytopathogens (Iqbal and Poór 2025).

Thus, our results confirmed the strong potential of the application of LED light spectra as an effective tool for optimizing photosynthetic function and secondary metabolism in plants. At the same time, combined spectra based on the ratios of red, blue, and photosynthetically active radiation were more effective in maintaining normal photosynthetic processes and a high level of protective antioxidants than monochrome LED light. Similar statements are also made by other authors. In particular, Goswami et al. (2023) showed that the combination of red and blue LED lights in a ratio of 50R : 50B was optimal for growth responses, photosynthetic performance, specialized metabolites synthesis (viz. myristicin (phenylpropene),

psi-limonene,  $\alpha$ -phellandrene, and chlorogenic acid), and nutritional quality in *Anethum graveolens*. Combined application of red, green, and blue light was shown to be the most efficient in promoting the synthesis of photosynthetic pigments and formation of new roots in *Kaempferia parviflora*, while combined application of red and blue was the most effective in stimulating shoot growth, carbohydrate, and protein synthesis (Hew et al., 2024). Combined red and blue lights resulted in the maximum glandular trichome density and promoted the growth and synthesis of major specialized metabolites in *Mentha spicata* L. (Chatterjee et al., 2025). The combined application of red and blue light in the ratio 3R : 1B was the most effective in enhancing photosynthesis, growth, and the accumulation of alkaloids such as indigo and indirubin, nucleosides (uridine, guanosine, and adenosine), and sugars in *Isatis tinctoria* L. While amino acids and organic acids synthesis were stimulated by 1R : 3B (Zhang et al., 2025).

## Conclusions

Our results confirmed the positive effect of the supplemental red and blue LED lighting on photosynthesis and secondary metabolism of seedlings of woody ornamentals of *M. × soulangeana*, *M. kobus*, *G. biloba*, *Rh. catawbiense* and *P. sylvestris* grown under shading conditions. The heliophytes *M. × soulangeana*, *M. kobus*, *G. biloba* and *P. sylvestris* demonstrated the highest photosynthetic pigments and tannin content when exposed to supplemental red LED lighting, while synthesis of flavonoids and anthocyanins were the most effectively stimulated by blue or red-blue LED lighting. Shade-tolerant *Rh. catawbiense* had the highest content of photosynthetic pigments when exposed to supplemental red-blue LED lighting. While the synthesis of protective antioxidants such as flavonoids and anthocyanins, was stimulated by monochrome red and blue LED lighting, respectively. To conclude, the supplemental LED lighting with red and blue spectra could effectively be used for optimization of photosynthesis and secondary metabolism in urban trees suffering from natural light deficiency.

## Conflict of interest

The authors have no competing interests to declare.

## Ethical statement

This article doesn't contain any studies that would require an ethical statement.

## Funding

The study was funded by the targeted scientific research program “Aerospace environmental observations in the interests of sustainable development and security” of the National Academy of Sciences of Ukraine, registration number 0121U111561.

## References

- Alrajhi, A. A., Alsahli, A. S., Alhelal, I. M., Rihan, H. Z., Fuller, M. P., Alsadon, A. A., & Ibrahim, A. A. (2023). The Effect of LED Light Spectra on the Growth, Yield and Nutritional Value of Red and Green Lettuce (*Lactuca sativa*). *Plants*, 12, 463. <https://doi.org/10.3390/plants12030463>
- Arcioni, S., Bovone, T., Damiani, F., & Paolucci, F. (2005). Light intensity is positively correlated with the synthesis of condensed tannins in *Lotus corniculatus*. In *XX International Grassland Conference: Offered papers* (p. 244). [https://doi.org/10.3920/978-90-8686-552-9\\_178](https://doi.org/10.3920/978-90-8686-552-9_178)
- Benincasa, P., Tosti, G., Farneselli, M., Maranghi, S., Bravi, E., Marconi, O., Falcinelli, B., & Guiducci, M. (2020). Phenolic content and antioxidant activity of einkorn and emmer sprouts and wheatgrass obtained under different radiation wavelengths. *Annals of Agricultural Sciences*, 65, 68–76. <https://doi.org/10.1016/j.aogas.2020.02.001>
- Chatterjee, D., & Mitra, A. (2025). Unlocking the potential of spectral LED lights in enhancing glandular trichome density and accumulation of bioactive specialized metabolites in spearmint. *Journal of Photochemistry and Photobiology B: Biology*, 271, 113239. <https://doi.org/10.1016/j.jphotobiol.2025.113239>
- Demotes-Mainard, S., Péron, T., Corot, A., Bertheloot, J., Le Gourrierec, J., Pelleschi-Travier, S., Crespel, L., Morel, P., Huché-Théliér, L., Boumaza, R., Vian, A., Guérin, V., Leduc, N., & Sakr, S. (2016). Plant responses to red and far-red lights, applications in horticulture. *Environmental and Experimental Botany*, 121, 4–21. <https://doi.org/10.1016/j.envexpbot.2015.05.010>
- Friulla, L., & Varone, L. (2025). Artificial light at night (ALAN) as an emerging urban stressor for tree phenology and physiology: A review. *Urban Science*, 9, 14. <https://doi.org/10.3390/urbansci9010014>
- Goswami, A., & Mitra, A. (2023). Light spectra manipulation stimulates growth, specialized metabolites and nutritional quality in *Anethum graveolens*. *Journal of Photochemistry and Photobiology B: Biology*, 249, 112812. <https://doi.org/10.1016/j.jphotobiol.2023.112812>
- Guo, X., Shakeel, M., Wang, D., Qu, C., Yang, S., Ahmad, S., & Song, Z. (2022). Metabolome and transcriptome profiling unveil the mechanisms of light-induced anthocyanin synthesis in rabbiteye blueberry (*Vaccinium ashei*: Reade). *BMC Plant Biology*, 22. <https://doi.org/10.1186/s12870-022-03585-x>
- Hashimoto, H., Sugai, Y., Uragami, C., Gardiner, A. T., & Cogdell, R. J. (2015). Natural and artificial light-harvesting systems utilizing the functions of carotenoids. *Journal of Photochemistry and Photobiology C: Photochemistry Reviews*, 25, 46–70. <https://doi.org/10.1016/j.jphotochemrev.2015.07.004>
- Hassanpour, S., Maherisis, N., & Eshratkhah, B. (2011). Plants and secondary metabolites (Tannins): a review. *International Journal for Soil Erosion*, 1, 47–53.
- Hew, W.H., Thien, V.Y., Rahman, Z.A., Pang, W.Q., Subramaniam S., & Tan, S. T. (2024). Effects of the spectrum of different light-emitting diodes (LEDs) on the morphological and physiological condition of *Kaempferia parviflora* plants. *South African Journal of Botany*, 172, 227–235. <https://doi.org/10.1016/j.sajb.2024.07.014>
- Hiscox, J. D., & Israelstam, C.F. (1979). A method for the extraction of chlorophyll from leaf tissue without maceration. *Canadian Journal of Botany*, 57, 1332–1334. <https://doi.org/10.1080/23311932.2019.1670553>
- Hofland-Zijlstra, J. D., & Berendse, F. (2009). The effect of nutrient supply and light intensity on tannins and mycorrhizal colonisation in Dutch heathland ecosystems. *Plant Ecology*, 201, 661–675. <https://doi.org/10.1007/s11258-008-9554-3>
- Hooks, T., Sun, L., Kong, Y., Masabni, J., & Niu, G. (2022). Short-term pre-harvest supplemental lighting with different light emitting diodes improves greenhouse lettuce quality. *Horticulturae*, 8(5), 435. <https://doi.org/10.3390/horticulturae8050435>
- Idris, A., Cuevas Linatoc, A., Abu bakar, M. F., Takai, Z.I., & Audu, Y. (2018). Effect of light quality and quantity on the accumulation of flavonoid in plant species. *Journal of Science and Technology*, 10(3), 32–45.
- Iqbal, N., & Poór, P. (2025). Plant protection by tannins depends on defense-related phytohormones. *Journal of Plant Growth Regulation*, 44, 22–39. <https://doi.org/10.1007/s00344-024-11291-1>
- Jaakola, L. (2013). New insights into the regulation of anthocyanin biosynthesis in fruits. *Trends in Plant Science*, 18(9), 477–483. <https://doi.org/10.1016/j.tplants.2013.06.003>
- Jokic, L., Pappert, I., Khanh, T. Q., & Kaldenhoff, R. (2025). Effect of light intensity and light spectrum of LED light sources on photosynthesis and secondary metabolite synthesis in *Ocimum basilicum*. *Plants*, 14, 1334. <https://doi.org/10.3390/plants14091334>
- Jung, E. S., Lee, S., Lim, S.-H., Ha, S.-H., Liu, K.-H., & Lee, C. H. (2013). Metabolite profiling of the short-term responses of rice leaves (*Oryza sativa* cv. Ilmi) cultivated under different LED lights and its correlations with antioxidant activities. *Plant Science*, 210, 61–69. <https://doi.org/10.1016/j.plantsci.2013.05.004>
- Lee, M., Rivard, C., Pliakoni, E., Wang, W., & Rajashekar, C. (2021). Supplemental UV-A and UV-B affect the nutritional quality of lettuce and tomato: health-promoting phytochemicals and essential nutrients. *American Journal of Plant Sciences*, 12, 104–126. <https://doi.org/10.4236/ajps.2021.121007>
- Li, Q., & Kubota, C. (2009). Effects of supplemental light quality on growth and phytochemicals of baby leaf

- lettuce. *Environmental and Experimental Botany*, 67, 59–64. <https://doi.org/10.1016/j.envexpbot.2009.06.011>
- Li, X., Lu, W., Hu, G., Wang, X.C., Zhang, Y., Sun, G.X., & Fang Z. (2016). Effects of light-emitting diode supplementary lighting on the winter growth of greenhouse plants in the Yangtze River Delta of China. *Botanical Studies*, 57, 2. <https://doi.org/10.1186/s40529-015-0117-3>
- Li, Z., & Ahammed, G. J. (2023). Plant stress response and adaptation via anthocyanins: A review. *Plant Stress*, 10, 100230. <https://doi.org/10.1016/j.stress.2023.100230>
- Lu, N., Maruo, T., Johkan, M., Hohjo, M., Tsukagoshi, S., Ito, Y., Ichimura, T., & Shinohara, Y. (2012). Effects of supplemental lighting within the canopy at different developing stages on tomato yield and quality of single-truss tomato plants grown at high density. *Environmental Control in Biology*, 50(1), 1–11. <https://doi.org/10.2525/ecb.50.1>
- Maham, N., Chamani, E., Mohebodini, M., & Tariverdizadeh, N. (2025). Optimizing biosynthesis: the role of LED light spectra in regulating phenolic and flavonoid accumulation in *Matricaria chamomilla* L. root cultures. *BMC Plant Biololy*, 25, 1573. <https://doi.org/10.1186/s12870-025-07609-0>
- Marchant, M. J., Molina, P., Montecinos, M., Guzmán, L., Balada, C., & Castro, M. (2022). Effects of LED light spectra on the development, phytochemical profile, and antioxidant activity of *Curcuma longa* from Easter Island. *Plants*, 11(20), 2701. <https://doi.org/10.3390/plants11202701>
- Mardar, M. R., & Serdyuk, L. V. (2008). *Methodological instructions for performing laboratory works on the course "Commodity science of phytoproducts" (Module VI) for students of specialty 6.030510*. Odesa National Academy of Food Technologies.
- Mohd Yusof, F. F., Yaacob, J. S., Osman, N., Ibrahim, M. H., Wan-Mohtar, W. A. A. Q. I., Berahim, Z., & Mohd Zain, N. A. (2021). Shading effects on leaf gas exchange, leaf pigments and secondary metabolites of *Polygonum minus* Huds., an aromatic medicinal herb. *Plants*, 10, 608. <https://doi.org/10.3390/plants10030608>
- Naznin, M. T., Lefsrud, M., Gravel, V., & Azad, M. O. K. (2019). Blue light added with red LEDs enhance growth characteristics, pigments content, and antioxidant capacity in lettuce, spinach, kale, basil, and sweet pepper in a controlled environment. *Plants*, 8, 93. <https://doi.org/10.3390/plants8040093>
- Neugart, S., Krumbein, A., & Zrenner, R. (2016). Influence of light and temperature on gene expression leading to accumulation of specific flavonol glycosides and hydroxycinnamic acid derivatives in kale (*Brassica oleracea* var. *sabellica*). *Frontiers of Plant Science*, 7. <https://doi.org/10.3389/fpls.2016.00326>
- Nowruzzi, B., Talebi, A., Beiranvand, H., & Salehi M. (2025). The effect of LED light irradiation and phosphate concentrations on the biological activity of *Fischerella* sp. *Discover Applied Sciences*, 7, 1055. <https://doi.org/10.1007/s42452-025-07730-7>
- Orlando, M., Trivellini, A., Puccinelli, M., Ferrante, A., Incrocci, L., & Mensuali-Sodi, A. (2022). Increasing the functional quality of *Crocus sativus* L. by-product (tepals) by controlling spectral composition. *Horticulture, Environment and Biotechnology*, 63, 363–373. <https://doi.org/10.1007/s13580-021-00407-1>
- Paradiso, R., & Proietti, S. (2022). Light-quality manipulation to control plant growth and photomorphogenesis in greenhouse horticulture: the state of the art and the opportunities of modern led systems. *Journal of Plant Growth Regulation*, 41, 742–780. <https://doi.org/10.1007/s00344-021-10337-y>
- Park, Y., & Runkle, E. S. (2018). Spectral effects of light-emitting diodes on plant growth, visual color quality, and photosynthetic photon efficacy: White versus blue plus red radiation. *PLoS ONE*, 13(8), e0202386. <https://doi.org/10.1371/journal.pone.0202386>
- Pavliuchenko, N. A., Didyk, N. P., & Li, L. (2021). Colorimetric methods for the analysis of allelopathically active substances in plant material and soil. In N. V. Zaimenko (Ed.), *Modern methods in allelopathic studies: Methodological manual* (pp. 117–147). Lira-K Publishing House. [In Ukrainian]
- Petrushkevych, Y. M., & Korshykov, I. I. (2020). Ecological and biological characteristics of *Betula pendula* in the conditions of urban environment *Regulatory Mechanisms in Biosystems*, 11(1), 29–36. <https://doi.org/10.15421/022004>
- Qiao, J., Hu, W., Chen, S., Cui, H., Qi, J., Yu, Y., Liu, S., & Wang, J. (2025). Effect of LED lights on morphological construction and leaf photosynthesis of lettuce (*Lactuca sativa* L.). *Horticulturae*, 11, 43. <https://doi.org/10.3390/horticulturae11010043>
- Qin, Y., Liu, X., Li, C., Chu, Q., Cheng, S., Su, L., Shao, D., Guo, X., He, Z., & Zhou, X. (2024). Effect of light intensity on celery growth and flavonoid synthesis. *Frontiers of Plant Science*, 16(14), 1326218. <https://doi.org/10.3389/fpls.2023.1326218>
- Sena, S., Kumari, S., Kumar, V., & Husen, A. (2024). Light emitting diode (LED) lights for the improvement of plant performance and production: A comprehensive review. *Current Research in Biotechnology*, 7, 100184. <https://doi.org/10.1016/j.crbiot.2024.100184>
- Shen, Y., Mao, L., Zhou, Y., Sun, Y., Liu, Z., & Liang, C. (2023). Integrated transcriptome and metabolome analysis revealed the molecular mechanism of anthocyanin synthesis in purple leaf pepper (*Capsicum annuum* L.) under different light intensities. *Horticulturae*, 9, 814. <https://doi.org/10.3390/horticulturae9070814>
- Shoji, K., Goto, E. I., Hashida, S. H., Goto, F. U., & Yoshihara T. (2010). Effect of red light and blue light on the anthocyanin accumulation and expression of anthocyanin biosynthesis genes in red-leaf lettuce. *Journal of Agricultural Sciences and Technology*, 22(2), 107–113. <https://doi.org/10.2525/shita.22.107>

- Smith, H. L., McAusland, L., & Murchie, E. H. (2017). Don't ignore the green light: exploring diverse roles in plant processes. *Journal of Experimental Botany*, 68(9), 2099–2110. <https://doi.org/10.1093/jxb/erx098>
- Talib, N. S., Jamaludin, D., & Abdul Malek, N. S. (2020). Effect of light emitting diode (LED) spectra on plant growth. *Advances in Agricultural and Food Research Journal*, 1(2): a0000135. <https://doi.org/10.36877/aafrj.a0000135>
- Trivellini, A., Toscano, S., Romano, D., & Ferrante, A. (2023). The role of blue and red light in the orchestration of secondary metabolites, nutrient transport and plant quality. *Plants (Basel)*, 12(10), 2026. <https://doi.org/10.3390/plants12102026>
- Wei, Y., Wang, S., & Yu, D. (2023). The role of light quality in regulating early seedling development. *Plants (Basel)*, 12(14), 2746. <https://doi.org/10.3390/plants12142746>
- Wellburn, A. R. (1994). The spectral determination of chlorophylls *a* and *b*, as well as total carotenoids, using various solvents with spectrophotometers of different resolution. *Journal of Plant Physiology*, 144(3), 307–313. [https://doi.org/10.1016/s0176-1617\(11\)81192-2](https://doi.org/10.1016/s0176-1617(11)81192-2)
- Yan, J., Lu, Y., & Yan, S. (2014). The effects of irradiance on the production of phenolic compounds and condensed tannins in *Larix gmelinii* needles. *Biologia plantarum*, 58. 159–163. <https://doi.org/10.1007/s10535-013-0367-4>
- Zhang, W., Song, X., Tang, H., Guan, X., Jin, L., Hu, J., Zheng, C., & Tang, Z. (2025). Synergistic enhancement of biomass and pharmacologically active metabolites in *Isatis tinctoria* L. via optimized red-blue LED supplemental lighting. *Plant Physiology and Biochemistry*, 229, Part B, 110439. <https://doi.org/10.1016/j.plaphy.2025.110439>
- Zhen, S., & Bugbee, B. (2020). Far-red photons have equivalent efficiency to traditional photosynthetic photons: Implications for redefining photosynthetically active radiation. *Plant, Cell & Environment*, 43(5), 1259–1272. <https://doi.org/10.1111/pce.13730>
- Zhu, X., Wu, C., & Hui, J. (2025). Effect of light intensity on anthocyanin synthesis assessed using leaves of *Aglaonema commutatum*. *Genes*, 16(4), 375. <https://doi.org/10.3390/genes16040375>
- Zhu, Y., Patil, B.S., & Zhen, S. (2025). From ultraviolet-B to red photons: Effects of end-of-production supplemental light on anthocyanins, phenolics, ascorbic acid, and biomass production in red leaf lettuce. *PLoS One*, 20(7), e0328303. <https://doi.org/10.1371/journal.pone.0328303>