


REVIEW

“Metabolight”: how light spectra shape plant growth, development and metabolism

Giulia Lauria¹ | Costanza Ceccanti¹ | Ermes Lo Piccolo²  | Hafsa El Horri¹ |
Lucia Guidi¹ | Tracy Lawson³ | Marco Landi¹ 

¹Department of Agriculture, Food and Environment, University of Pisa, Pisa, Italy

²Department of Agriculture, Food, Environment and Forestry, University of Florence, Florence, Italy

³School of Life Sciences, University of Essex, Colchester, Essex, United Kingdom

Correspondence

Marco Landi,
Email: marco.landi@unipi.it

Edited by A. Krieger-Liszkay

Abstract

Innovations in light technologies (i.e. Light Emitting Diodes; LED) and cover films with specific optical features (e.g. photo-selective, light-extracting) have revolutionized crop production in both protected environments and open fields. The possibility to modulate the light spectra, thereby enriching/depleting cultivated plants with targeted wavebands has attracted increasing interest from both basic and applicative research. Indeed, the light environment not only influences plant biomass production but is also a pivotal factor in shaping plant size, development and metabolism. In the last decade, the strict interdependence between specific wavebands and the accumulation of targeted secondary metabolites has been exploited to improve the quality of horticultural products. Innovation in LED lighting has also marked the improvement of streetlamp illumination, thereby posing new questions about the possible influence of light pollution on urban tree metabolism. In this case, it is urgent and challenging to propose new, less-impacting solutions by modulating streetlamp spectra in order to preserve the ecosystem services provided by urban trees. The present review critically summarizes the main recent findings related to the morpho-anatomical, physiological, and biochemical changes induced by light spectra management *via* different techniques in crops as well as in non-cultivated species. This review explores the following topics: (1) plant growth in monochromatic environments, (2) the use of greenhouse light supplementation, (3) the application of covering films with different properties, and (4) the drawbacks of streetlamp illumination on urban trees. Additionally, it proposes new perspectives offered by *in planta* photomodulation.

1 | INTRODUCTION

Sunlight is the energy that powers life on our planet as photosynthesis is the “green engine” that converts the electromagnetic energy of sunlight into chemical energy by fixing carbon dioxide and water into sugars. Wavelengths of the electromagnetic spectrum absorbed by

plants and used to drive photosynthesis can be grouped into (1) ultra-violet (UV) ranging from 100–400 nm (i.e. UV-A 100–280 nm; UV-B 280–315 nm; UV-C 315–400), a region in which photons are associated with potentially damaging high energy, (2) photosynthetically active radiation (PAR; 400–700 nm), corresponding to the wavebands that are principally absorbed by plant pigments to fuel the

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2024 The Author(s). *Physiologia Plantarum* published by John Wiley & Sons Ltd on behalf of Scandinavian Plant Physiology Society.

photosynthetic machinery, and (3) far-red (FR) light, associated with lower-energy photons.

From the first water-to-land transition and the consequent land colonization, plants had to face a set of variable life conditions, including the light environment. Being sessile organisms, they have adapted to light intensity (low/high), light fluctuation, and continuous light (at high latitude) and have evolved to efficiently perceive light quality, intensity, direction, and timing, then transmit and process the information received from light stimuli to optimize the plant development and behaviour (Carvalho et al., 2011). Through photoreceptors, namely phytochromes (dimeric chromopeptides that possess two photoconvertible forms for R and FR perception), cryptochromes (devoted to blue and UV absorption), and phototropin (flavoproteins mediating blue, UV and green light absorption), as well as UV-dedicated receptors (i.e., UV Resistance Locus 8 – UVR8, for sensing UV-A and UV-B) plants regulate photomorphogenesis, photoperiodicity and phototropism, but also maximize light harvesting in the context of competition with neighbouring plants or in shade condition in the understorey. (Rizzini et al., 2011; Landi et al., 2020; Rai et al., 2021). For example, phytochromes that are sensitive to variation in red/far red (R/FR) ratio (Falcatore & Bowler, 2005) are determinants in germination, de-etiolation, shade avoidance, and flowering responses in land plants (Mathews, 2006).

In terms of light harvesting and utilization, plants have evolved finely tuned and well-orchestrated mechanisms aimed at, on the one hand, maximizing light harvesting under suboptimal light conditions and, on the other hand, protecting the photosynthetic apparatus when light is in excess of what can be used for photosynthetic requirements (namely, photoinhibition) (Baker, 2008). In plants, light-harvesting pigments, chlorophyll *a* and *b* (which absorb principally in the red and blue regions of the solar spectrum) and the accessory pigments carotenoids (which extend the absorbed light to other wavelengths in the visible spectrum) are devoted to intercepting the sunlight and transferring electromagnetic energy to the reaction centers of both photosystems. The red and blue portions of the spectrum are the most absorbed by chlorophylls, but regardless of all the wavelengths of light they absorb, chlorophylls exclusively utilize red photons to drive water-splitting and ferredoxin-reducing photochemistry. (Björn et al., 2009). Indeed, the extra energy of a blue photon, according to the Planck equation (75% higher comparing a 400 vs a 700 nm photon), is dissipated as heat within subpicoseconds to the same energy level as red (Björn et al., 2009).

Curiously, the leaf's green appearance has spread the misconception that green light is poorly absorbed and utilized by the plant. Actually, green light (GL) plays a pivotal role in photosynthesis in the deepest mesophyll layers as well as in the understorey, where light is depleted in the red and blue regions due to absorbance by the overhanging leaves (Folta & Maruhnich, 2007; Brodersen & Vogelmann, 2010). Indeed, though red and blue are peaks for chlorophyll absorption, leaf reflectance, light scattering and energy loss via thermal dissipation dramatically reduce the efficiency of energy conversion to 4.6% in C3 and around 6% in C4 species (Zhu et al., 2008). Moreover, GL is also perceived by phytochromes and cryptochromes, reversing the effect of blue light, for

example, in terms of stomatal regulation (Frechilla et al., 2000; Kim et al., 2004). Additionally, in red-leaved species, the effect of GL might be different due to the presence of red pigments (i.e., anthocyanins), which absorb preferentially (but not exclusively) in the green portion of the solar spectrum (Landi et al., 2021; Simkin et al., 2022).

In view of the above, in the last decade the management of light regimes and spectra has been explored to (1) promote plant growth and maximize biomass production in indoor cultivation (Jones, 2018; Stamford et al., 2023), (2) shape plant size and architecture (Li et al., 2000; Stapel et al., 2011), (3) improve the nutritional value of fruit and vegetables (Jones, 2018; He et al., 2022; Sarabi et al., 2022), (4) modulate the biosynthesis of targeted secondary metabolites (Lobiuc et al., 2017; Landi et al., 2020; Morello et al., 2022). Technical advancements in artificial lighting, i.e. the development of LED technology (Singh et al., 2015; Stamford et al., 2023) and new material developed for cover films (Cerny et al., 2003; Manja & Aoun, 2019; Zheng et al., 2020; Liu et al., 2022) have further improved the capacity of modifying the light environment perceived by the plant. In addition, there are some cases in which the modulation of the light regime may exert unwanted effects on plant performance, for example, the possible side effect of continuous light from streetlamps in urban environments (Matzke, 1936; Chaney, 2002; Ffrench-Constant et al., 2016; Massetti, 2018; Lo Piccolo et al., 2023); thus the new LED technology can be employed to minimize the light disturbance on urban trees physiology and phenology.

The present review summarizes the main findings related to morpho-anatomical, physiological and biochemical changes promoted by specific light regimes (Figure 1), i.e., the growth of plants in monochromatic environments (section 2), the use of light supplementation (section 3) as well as covering films with different features (photo-selective, light-extracting, diffusive, mulching films – section 4). In addition, in section 5, we depicted how streetlamp illumination may influence morpho-anatomy and physio-chemical attributes of urban trees with the aim of increasing awareness of the necessity of less-impacting streetlamp solutions.

2 | MORPHO-ANATOMICAL TRAITS AND PLANT SECONDARY METABOLITES IN MONOCHROMATIC ENVIRONMENTS

The effect of monochromatic light (ML) on plant biomass, morpho-anatomical traits, and secondary metabolite production has been extensively investigated in the last decade. Table 1 and Figure 2 summarize the results from recent studies dealing with the effect of ML environments to unveil ML-triggered *in planta* metabolic changes, whose comprehension is crucial not only for improving horticultural crop yield and quality, as reviewed by Jones (2018), but also to photomodulate the synthesis of targeted bioactive compounds in medicinal plants, such as *Cannabis sativa* (Danziger & Bernstein, 2021; Wei et al., 2021; Morello et al., 2022), *Withania somnifera* (Adil et al., 2019), *Scutellaria baicalensis* (Zhang et al., 2022a), *Aronia* spp. (Szopa et al., 2018), *Artemisia absinthium* (Tariq et al., 2014), *Moringa oleifera* (Bajwa et al., 2023).

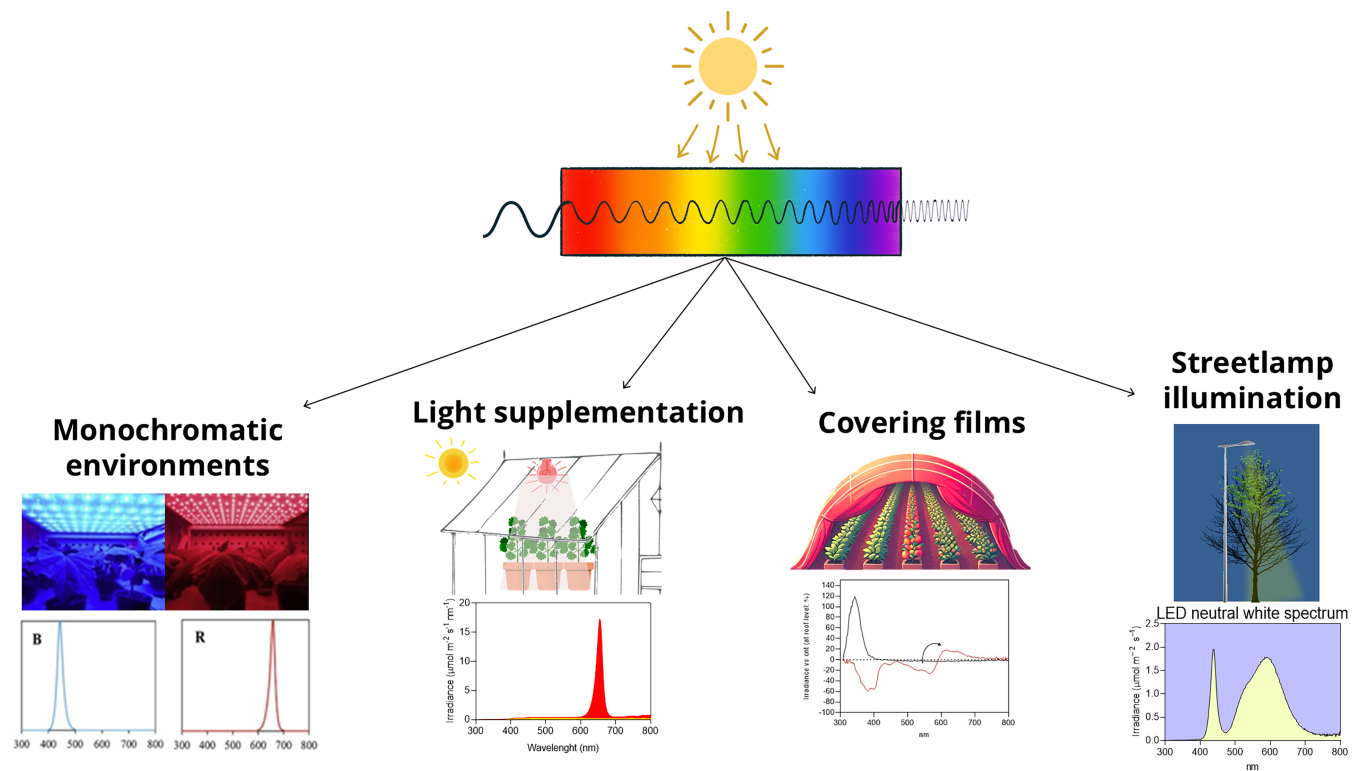


FIGURE 1 Light management techniques explored in the present review: monochromatic environments (section 2), light supplementation (section 3), covering films with different features (section 4), and the streetlamp illumination on urban trees (section 5).

The effects of monochromatic red light (RL) and blue light (BL) environments have attracted intensive research. Under short photoperiods of red and blue light, cryptochromes and phyB act synergistically, but under continuous exposure to the same light field, the actions of phyB and cryptochrome can become independent and additive (Casal, 2000). Therefore, the behaviour of plants under monochromatic RL or BL is not easily predictable and, as depicted below, may lead to species-specific as well as dose-dependent responses (Ahmad et al., 2016; Kitayama et al., 2019; Khurshid et al., 2020; Izzo et al., 2021; Rong Sng et al., 2021; Wei et al., 2021; Carillo et al., 2022; Zhang et al., 2022a; Su et al., 2024). RL is able to enhance plant/callus biomass production, as observed in plants of *Withania somnifera* (Adil et al., 2019), *C. sativa* (Wei et al., 2021), *Coriandum sativum* (Nguyen et al., 2020), *Lactuca sativa* (Izzo et al., 2021), *Mesembryanthemum crystallinum* (Kim et al., 2018), *I. aquatica* (Kitayama et al., 2019), *Scutellaria baicalensis* (Zhang et al., 2022a), *Brassica oleracea*, (Sathasivam et al., 2023), callus of *S. rabaudiana*, (Ahmad et al., 2016) and *in vitro* cultures of *Pistacea vera* (Abdouli et al., 2023). Greater stem diameter, leaf area, leaf length, and overall plant weight are the most common morpho-anatomical traits observed after red light (RL) exposure, which explains the higher biomasses seen in plants exposed to this light condition. (Kim et al., 2018; Kitayama et al., 2019; Nguyen et al., 2020; Rong Sng et al., 2021; Carillo et al., 2022; Morello et al., 2022; Abdouli et al., 2023; Su et al., 2024; Wei et al., 2021). Given that phytochromes are present in two forms: the inactive form, which absorbs maximally in RL (Pr) and the active

form, which absorbs maximally in far-red (FR) light (Pfr), the increase in plant biometric traits is conceivably related to a combination of increment of the active form of phytochromes as well as the interception of the most efficient wavebands for photosynthesis (McCree, 1972). RL is principally absorbed by PSII, whilst FR light is preferentially absorbed by PSI, so the use of monochromatic RL may lead to overexcitation of PSII. Therefore, neither of the two lights would be optimal for photosynthesis when applied alone, and the interaction between the two lights would be synergistic and has to be considered when growing plants under monochromatic RL (Zhen & van Iersel, 2017). Indeed, the supplementation of FR to white light (up to 40% of background light) can increase the canopy's gross photosynthesis by adding an equivalent amount of white photons (Zhen & Bugbee, 2020).

Though a huge body of evidence supports the accumulation of biomass in plants exposed to RL, contrasting results have emerged regarding the RL-dependent biosynthesis of secondary metabolites that are of utmost importance for human health. For example, Adil et al. (2019) found the highest content of chlorogenic acid and withaferin A in callus cultures of *W. somnifera* grown in an RL environment. These authors hypothesized that withanolides, such as withaferin A, are involved in the conversion of phenylalanine to cinnamic acid catalyzed by phenylalanine ammonia-lyase (PAL). This enzyme is activated under red light (RL), signalling the phenylpropanoid pathway to counteract oxidative stress by accumulating higher levels of withanolides (Adil et al., 2019). Enhancement of PAL activity, the key enzyme of

TABLE 1 Effect of monochromatic LED lights on productivity and on different morpho-anatomical and secondary molecular traits compared to polychromatic light effects. Effects are referred to control treatment which is the first indicated in the light recipe list. Cnt – control; R – red light, FR – far-red light; B – blue light, G – green light; V – violet light; W – white light; Y – yellow light; TPC – total phenolic content, TFC – total flavonoid content; HPS – high pressure sodium; PAL – phenylalanine ammonia lyase.

Species	Light recipe	Intensity	Duration	Effects	Reference
<i>Aronia melanocarpa</i> , <i>Aronia arbutifolia</i> , <i>Aronia × prunifolia</i> in vitro seedlings	W, UV-A irradiation (315–400 nm), B (450–492 nm), R (647–770 nm), FR (770–800 nm), dark condition	20 and 60 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h/8 h, 4 weeks	B ↑ shoot biomass, phenolic acid and flavonoid content	Szopa et al. (2018)
<i>Artemisia absinthium</i> callus cultures	Cool-W light (380–780 nm), B (380–560 nm), G (480–670 nm), Y (530–780 nm), R (610–715 nm), dark condition	40–50 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h/8 h, 3 weeks	R ↑ peroxidase activity, protease activity, total protein content, and chlorophyll <i>a/b</i> ratio G ↑ chlorophyll and carotenoid content, TPC, TFC, and antioxidant activity Y ↑ of malondialdehyde content	Tariq et al. (2014)
<i>Artemisia argyi</i> seedlings	W, B (455 nm), R light (660 nm), R:B 1:3	160 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 14 h/10 h, 21 days	R ↑ root number, root length, plant height, chlorogenic acids content. B ↑ leaf area, TPC in the first sampling (7th day; decreasing with time), TFC; ↓ plant height	Su et al. (2023)
Broccoli (<i>Brassica oleracea</i>) sprouts	B (450 nm), R (660 nm), R + B, R + UVA (for UVA peak at 365 nm)	50 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod: 16 h/8 h, 5 days	B ↑ cotyledon anthocyanin content, TPC, TFC, and ascorbic acid content R + B ↑ hypocotyl anthocyanin content, TPC, TFC, and ascorbic acid content	Yang et al. (2021)
Red <i>Brassica oleracea</i> var. <i>gongyloides</i> sprouts	W light (449–551 nm), R (636 nm), B	90 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h/8 h, 10 days	R ↑ fresh weight. B ↑ shoot and root lengths, phenylpropanoid and glucosinolates contents	Sathasivam et al. (2023)
<i>Cannabis sativa</i> inflorescences	HPS W light, B (430 nm), R (630 nm), Rose (430 + 630 nm, ratio 1:10), V (430 + 630 nm, ratio 2:1), and Amber (595 nm)	250– 270 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Vegetation stage: photoperiod 18 h, 0–13 days. Flowering stage: 12 h, 8 weeks	Amber and R ↑ plant height; ↓ CBD concentrations. B ↑ THC, CBD and terpene concentration; ↓ fresh inflorescence biomass	Morello et al. (2022)
plants	HPS W light, R:B 9.30:1, R:B 9.20:1, R:B 1.61:1, R:B 6.47:1, R:B 7.15:1, R:B 16.8:1	R:B 9.30:1, 191 $\mu\text{mol m}^{-2} \text{s}^{-1}$, R:B 9.20:1, 129 $\mu\text{mol m}^{-2} \text{s}^{-1}$, R:B 1.61:1, 540 $\mu\text{mol m}^{-2} \text{s}^{-1}$, R:B 6.47:1, 28.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$, R:B 7.15:1, 41.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$, R:B 16.8:1, 252 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h/8 h, 110 days	R:B 1.61:1, R:B 6.47:1 ↓ stem diameter (+50%). R:B 9.20:1 and R:B 16.8:1 ↑ stem and root biomass (due to light intensity), cannabinoids content. B ↑ hemp flower biomass; ↓ biometrical parameters	Wei et al. (2021)
	W HPS light, W + R:B 1:1, W + B:R 1:1, W + B:R 1:4	Up to 950 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 12 h, 12 days for more vigorous varieties and	R:B 1:1 ↑ inflorescence yield and height. B:R 1:4 ↓ cannabigerolic acid accumulation	Danziger and Bernstein (2021)

TABLE 1 (Continued)

Species	Light recipe	Intensity	Duration	Effects	Reference
<i>Citrus reticulata</i> callus culture	W light, R, B, G, Y		24 days for the less vigorous variety Photoperiod 16 h/8 h for W, 24 h for the other light treatments, 4 weeks	W ↑ fresh biomass followed by G and B. R ↑ values for TPC, TFC, and antioxidant activity. B ↑ activity of antioxidant enzymes	Anum et al. (2021)
<i>Coriandrum sativum</i> microgreens	B, G, RB 87:13 and RBFr 81.5:12.5:6	200 ± 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h/8 h, 18 days	R, RB, and RBFr ↑ stem and leaf fresh weight. R ↑ ascorbic acid content. B ↑ antioxidant capacity and TPC. G ↓ leaf and stem fresh weight, antioxidant capacity and ascorbic acid content	Nguyen et al. (2020)
<i>Crocus sativus</i> plantlets	W light, 100% B, 75%B (75%B + 25%R), 50%B (50%B + 50% R), 25%B (25%B + 75%R), 100% R W (400–700 nm), B (465 nm), R (660 nm), and R:B 1:1 combined with GABA or GA3 treatment(multifactorial experiment)	150 ± 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$ 80 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 11 h/13 h, 18–22 days (until flowering) Photoperiod 16 h/8 h, until the end of the flowering period	R ↑ carotenoids concentration in petals. B ↑ flower number, flower fresh weight, anthocyanin, safranal and crocin content; earliest flowering B and R:B ↑ phytochemical content. B ↑ flower biomass, enhanced with GABA or GA3 treatment	Moradi et al. (2022) Eftekhari et al. (2023)
<i>Eclipta alba</i> callus culture	Cool W fluorescent tubes (400–700 nm), continuous Y (570 nm), G (510 nm), W (400–700 nm), B (460 nm), R (660 nm), dark conditions	40–50 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h/8 h for Cnt W and 24 h for the other light treatments, 28 days	R ↑ TPC, TFC, antioxidant activity and secondary metabolites (amyrin, stigmasterol, luteolin, coumarin, ecalbatin, wedelolactone, wedelolactone)	Khurshid et al. (2020)
<i>Ipomoea aquatica</i> plantlets	R:B (87:13), R, B, G, R:B:FR (81.5:12.5:6)	200 ± 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 14 h/10 h, 14 days	R ↑ stem length and fresh weight. B ↑ antioxidant activity capacity in leaves and stems; ↓ stem elongation	Kitayama et al. (2019)
<i>Lactuca sativiva</i> cv. 'Banchu Red Fire' seedlings	W fluorescent light; G (510–520–530 nm) W fluorescent light; B (470 nm), G1 (510 nm), G2 (520 nm), R (680 nm)	100, 200 and 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ 100 and 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 24 h light, 10 days Photoperiod 24 h, 7 days	G ↓ biomass; ↑ leaf area (+71%), fresh weight (+59%) in plants G510 PPF0300 than plants under PPF0200; ↑ petiole length at PPF0100 R ↑ sucrose. B ↑ amino acids, fatty acids, lipids, alpha-tocopherol, anthocyanins. G1 and G2 downregulation of flavonoids and the expression of genes involved in flavonoid biosynthesis and PAP2 gene.	Johkan et al. (2012) Kitazaki et al. (2018)
cv. 'Waldmann's Green' and 'Outredgeous' plantlets	Fluorescent W lamp, 100% R, B:R (7:93), B:R (26:74), B:R (66:34), 100% B	200 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h/8 h, 18 days	100% R ↑ shoot fresh mass. B 66% ↑ in leaf thickness and chlorophyll percentage	Izzo et al. (2021)

(Continues)

TABLE 1 (Continued)

Species	Light recipe	Intensity	Duration	Effects	Reference
<i>Batavia</i> plants cv. 'Batavia'	W fluorescent light, R:B 3:1, R:B 2:1, R:B:FR 3:1:0.5, R (660 nm), B (450 nm), and FR (730 nm)	R:B 3:1 - R 60 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and B 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$, R:B 2:1 - R 40 $\mu\text{mol m}^{-2} \text{s}^{-1}$, B 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$, R:B:FR 3:1:0.5 - R: 60 $\mu\text{mol m}^{-2} \text{s}^{-1}$, B 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$, FR 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h/8 h, 3 weeks	R \uparrow leaves and petioles. B \uparrow leaf area, \downarrow petioles. R:B \uparrow anthocyanins and carotenoids content	Rong Sng et al. (2021)
<i>Lepidium sativum</i> callus cultures	W light, R (660 nm), G (510 nm), B (460 nm), Y (570 nm), W (400–700 nm), dark condition	40–50 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h/8 h for W, 24 h for the other light treatments, 28 days	W \uparrow fresh and dry biomass, caffeic acid, ferulic acid, vanillic acid, sinapic acid, and protocatechuic acid content. W, B, and dark condition \uparrow antioxidant activity (95.1%, 94.2%, and 93.2%, respectively), quercetin and kaempferol concentrations. B \uparrow p-coumaric acid content	Asad Ullah et al. (2019)
<i>Linum usitatissimum</i> sprouts and microgreens	R:G:B 1:1:1, B (peak at 450 nm), R (peak at 660 nm), G (peak at 520 nm)	200 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 24 h light for 4 days, and 16 h/8 h for the next 7 days	B \uparrow TPC, TFC, chlorogenic acid content and antioxidant activity	Puccinelli et al. (2022)
<i>Mesembryanthemum crystallinum</i> plantlets	R (660 nm), B (450 nm)	120 or 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 14 h/10 h, 4 weeks	R \uparrow biomass and leaf area. B (150 $\mu\text{mol m}^{-2} \text{s}^{-1}$) \uparrow phytochemicals concentrations and antioxidant activity	Kim et al. (2018)
<i>Moringa oleifera</i> callus culture	W light (400–700 nm), continuous W (400–700 nm), Y (570 nm), R (660 nm), G (510 nm), and B (460 nm), dark conditions	40–50 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h/8 h for Cnt W and 24 h for the other light treatments, 28 days	B \uparrow biomass and photosynthetic pigment content, chlorogenic acid accumulation	Bajwa et al. (2023)
<i>Operculina turpethum</i> callus culture	Cool W fluorescent light, dark conditions, continuous W (400–700 nm), R (630 nm), G (520 nm), B (460 nm), and Y (570 nm)	40–50 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h/8 h for Cnt W and 24 h for the other light treatments, 35 days	B \uparrow DPPH antioxidant activity, followed by R and G light, gallic acid, quercetin, coumarin, salicylic acid. Dark and R \uparrow SOD and CAT activities	Biswal et al. (2022)
<i>Petroselinum crispum</i> cv. microgreens	RGB: 45% R (600–700 nm, peaking at 650 nm), 10% G (500–600 nm), 45% B (400–500 nm, peaking at 460 nm), B: 0% R, 10% G, 90% B; R: 90% R, 10% G, 0% B	300 \pm 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 12 h, 11 days	R \uparrow biomass, cotyledon, and petiole length; \downarrow thickness of spongy parenchyma tissue, number of intercellular spaces. B \uparrow compactness, higher ascorbic acid content and antioxidant activity; \downarrow height. RGB \uparrow polyphenol content; \downarrow photosynthetic pigments	Carillo et al. (2022)

TABLE 1 (Continued)

Species	Light recipe	Intensity	Duration	Effects	Reference
<i>Pistacea vera</i> in vitro plantlets (micro propagated by callus culture)	W fluorescent light, B, R, and BR (1:1)	40 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h/8 h, 6 weeks	R \uparrow biomass and stem elongation, \downarrow antioxidant activity. B: \uparrow TFC than R and BR treatments. BR \uparrow chlorophyll content, TPC	Abdouli et al. (2023)
<i>Raphanus sativus</i> , <i>Brassica rapa</i> cv. 'Nipposinica', <i>Cichorium intybus</i> , <i>Medicago sativa</i> , <i>Tagetes tenuifolia</i> and <i>Celosia plumosa argentea</i> microgreens	R6:B (65:35) and R:G:B (47:19:34)	110, 220 and 340 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h/8 h, 7 days	RGB \uparrow biomass and TPC than RB treatment	Orlando et al. (2022)
<i>Scutellaria baicalensis</i> seedlings	W light, B (460 nm), R (660 nm), and different combinations of R and B (R9B1, R7B3, R5B5, R3B7, and R1B9)	50 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h/8 h, 15 days	R \uparrow biomass of whole plant and root, increasing with the enhancement of R portion, \uparrow baicalin and wogonoside content. B \downarrow of plant growth, baicalin and wogonoside content. R9B1, R7B3 \uparrow accumulation of flavonoids	Zhang et al. (2022a)
<i>Solanum xanthocarpum</i> callus cultures	W, B (460 nm), W (400–700 nm), G (510 nm), R (660 nm), Y (570 nm), dark condition	45–50 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h/8 h for Cnt W and 24 h for the other light treatments, 5 weeks	Continuous W and B \uparrow biomass accumulation. B \uparrow TPC, methyl-cafeate, efficiency against alpha-glucosidase (41.92%) and alpha-amylase (29.63%) inhibition, more practical for enhanced anti-AGEs formation ability, \uparrow COX-1 inhibition %. W \uparrow flavonoid content. B and R \uparrow scopoletin and esculetin concentrations. R \uparrow 15-LOX inhibition %. Dark \uparrow antioxidant activity.	Usman et al. (2020)
<i>Stevia rebaudiana</i> callus cultures	W light (380–780 nm), G (480–670 nm), Y (530–780 nm), B (380–560 nm) and R (610–715 nm)	40–50 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h/8 h, 30 days	R \uparrow biomass accumulation. B \uparrow TPC, TFC and antioxidant activity	Ahmad et al. (2016)
<i>Vaccinium corymbosum</i> cv. 'Sunt Blue Giant' callus cultures from root or leaf origin	Dark, W, B and R	W 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$, B 120 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and R 180 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h/8 h, 12 days	R \uparrow anthocyanin content from root and leaf origin (5.7- and 4.9-fold higher respectively), qualitative composition of anthocyanins in callus obtained from leaf origin largely than in callus obtained from root origin, accumulation of flavonols, PAL activity	Abou El-Dis et al. (2021)
<i>Withania somnifera</i> callus culture	W fluorescent light; V (350–400 nm), B (380–560 nm), G (480–670 nm), Y (530–780 nm), R (610–715 nm)	50 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h/8 h, 5 weeks	R \uparrow callus biomass, TPC and TFC, chlorogenic acid and withaferin A content; V \uparrow TPC and TFC. G \uparrow withaferin A	Adil et al. (2019)

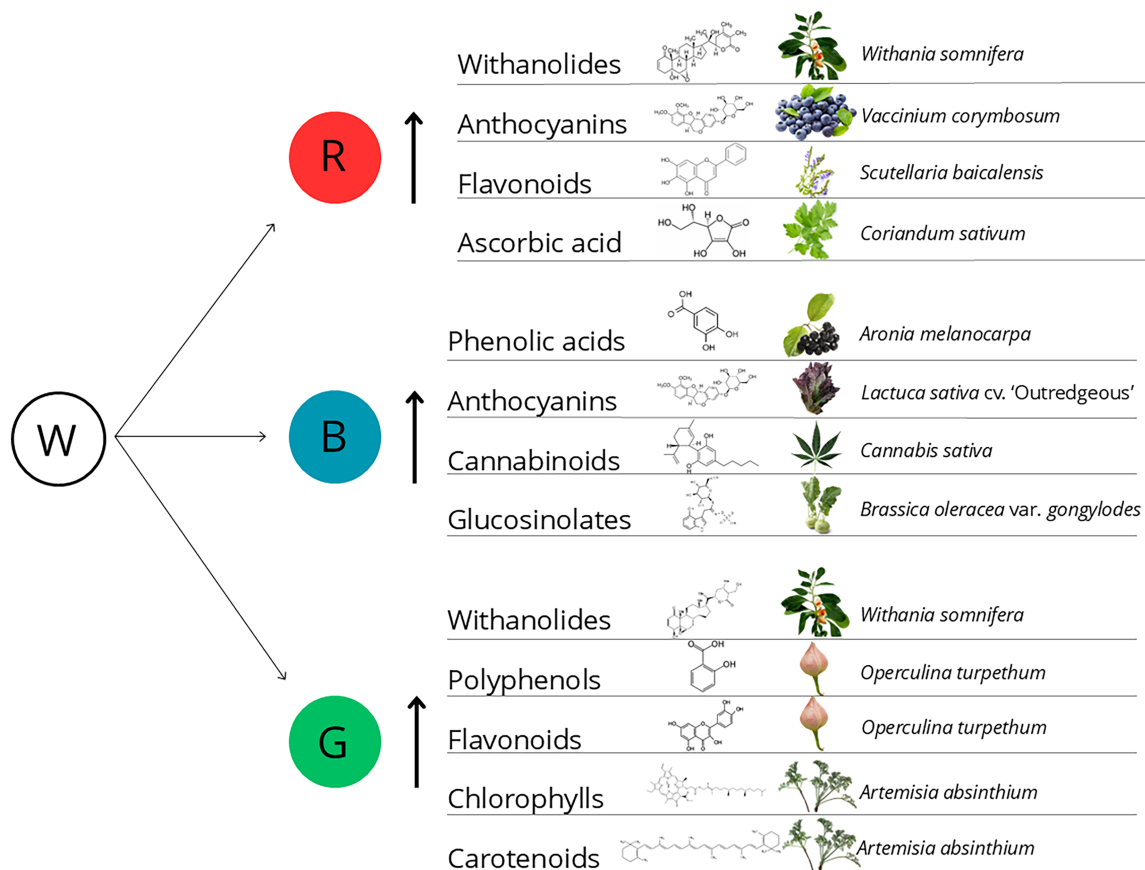


FIGURE 2 Summarization of monochromatic red (R), blue (B) and green (G) light effects (compared to that cool white light – W) on the biosynthesis of secondary metabolites in some plant species. A broader framework is extensively reported in Table 1.

the phenylpropanoid branch metabolism, promoted by RL might also explain the increase in anthocyanin and flavonol content in *Vaccinium corymbosum* callus cultures (Abou El-Dis et al., 2021). Zhang et al. (2022a) also observed an increased level of two other flavonoids, namely baicalein and wogonoside, in *S. baicalensis* seedlings supplied with RL. In the same study, a punctual transcriptome sequencing analysis demonstrated that RL induced a higher accumulation of flavonoids than other ML treatments. This effect was attributed to the upregulation of genes involved in flavonoid biosynthesis, such as PAL, cinnamate CoA ligase (CLL), chalcone synthase (CHS), flavonol synthase (FNS) and 8-O-methyl transferase (OMT). Moreover, the RL-promoted increased level of cytokinins may also contribute to the accumulation of phenolic compounds (Khurshid et al., 2020).

RL also promoted the accumulation of ascorbic acid in *C. sativum* microgreens (Nguyen et al., 2020), targeted secondary metabolites in *Eclipta alba* such as amyirin, stigmasterol, luteolin, coumarin, eclalbatin, wedelolactone and derivatives (Khurshid et al., 2020) as well as carotenoids in petals of *Crocus sativum* (Moradi et al., 2022). Despite the generally positive impact of RL in terms of cannabinoid accumulation (Wei et al., 2021), some authors reported a reduction of this class of compounds in some *C. sativa* varieties after RL treatment, highlighting the importance of considering the genotype-dependent responses in terms

of secondary metabolism modulation (Danziger & Bernstein, 2021; Morello et al., 2022).

Several studies have also analysed the effects of BL on plants, yielding interesting but occasionally contrasting results (Table 1). In terms of morpho-anatomical traits of plants treated with monochromatic BL, short petioles and shoots (with a reduction of plant height), leading to more compact plants characterized by increased leaf area and leaf thickness were observed (Izzo et al., 2021; Rong Sng, 2021; Carillo et al., 2022). In some studies, these changes translated into a reduction of the overall plant biomass (Zhang et al., 2022a; Wei et al., 2021). It is worth noting that such treatment led to enhanced inflorescence biomass in flowering crops (Wei et al., 2021; Orlando et al., 2023; Moradi et al., 2022). Rong Sng et al. (2021) analysed the morpho-anatomical traits of *Lactuca sativa* cv. Batavia plants grown for three weeks in a BL environment were found to have a higher leaf area and shorter petioles compared to lettuce grown in polychromatic or other MLs, such as RL and FR light. Accordingly, Carillo et al. (2022), analysing *Petroselinum crispum* microgreens grown in a chamber illuminated with BL, observed shorter internodes and more compact plants compared to those grown with other MLs or polychromatic lights. These authors attributed the inhibition of hypocotyl growth in plants exposed to BL to modifications in the cell wall

structure, resulting in reduced turgor and finally leading to a slower plant growth rate (Carillo et al., 2022).

Another topic of research on the effect of a BL environment on plants is the possibility of increasing the inflorescence biomass. This phenomenon has been specifically observed in *Cannabis sativa* and *C. sativus* (Wei et al., 2021; Eftekhari et al., 2020; Moradi et al., 2022), suggesting a species-specific explanation for this feature. In *C. sativa*, it was observed that BL increased the photosynthate accumulation in the inflorescence, thereby reducing the vegetative growth and promoting inflorescence development and yield (Wei et al., 2021). Moradi et al. (2022) provided new insights, elucidating that the BL photoreceptor CRY is capable of initiating flowering by controlling the CRY2/coat protein 1(COP1) complex. COP1, in turn, affects the dehydration of CONSTANS (CO), a zinc-finger transcription factor able to trigger plants to flower.

It has long been known that in response to biotic and abiotic stressors, plants synthesize an arsenal of secondary metabolites. Exposure to a monochromatic BL can represent a “eustress” for plants, thus a stress that activates and stimulates plant responses, with positive consequences for plant development (Lichtenthaler, 1996), for example, the stimulation of the biosynthesis of those targeted secondary metabolites whose accumulation is strictly dependent on the applied narrowband light. As illustrated in Table 1, several studies reported an increase in the concentrations of key antioxidant molecules and enhanced antioxidant activity in seedlings and/or callus cultures grown under monochromatic BL (Ahmad et al., 2016; Kim et al., 2018; Kitazaki et al., 2018; Szopa et al., 2018; Asad Ullah et al., 2019; Kitayama et al., 2019; Nguyen et al., 2020; Usman et al., 2020; Anum et al., 2021; Yang et al., 2021; Biswal et al., 2022; Carillo et al., 2022; Moradi et al., 2022; Morello et al., 2022; Puccinelli et al., 2022; Bajwa et al., 2023; Eftekhari et al., 2023; Sathasivam et al., 2023; Su et al., 2024). The highest observed total phenolic content (TPC) and total flavonoid content (TFC) in plants exposed to BL can be attributed to the proximity of B and UV spectra wavelengths, thus promoting similar stimulatory effects on secondary metabolite biosynthesis (Abdouli et al., 2023). This observation is corroborated by Szopa et al. (2018), who noted the highest accumulation of neochlorogenic and protochatecuic acids in *Aronia melanocarpa* grown under BL and UV-A monochromatic environment. Simultaneously, other researchers confirmed that cryptochromes (blue and UV receptors) play a pivotal role in regulating the biosynthesis of secondary metabolites such as anthocyanins, cannabinoids and glucosinolates (Mickens et al., 2018; Wei et al., 2021; Yang et al., 2021; Morello et al., 2022; Sathasivam et al., 2023).

Although fewer studies are available on the use of monochromatic green (GL) environments (compared to those dealing with BL and RL), GL has been generally proven to exert negative effects on plant growth, as revealed by the impairment of several morpho-anatomical parameters, including a reduced leaf number and area in relation to stem weight as well as lower stomata density (Table 1). Furthermore, starch granules in the chloroplasts were fewer in number and smaller in size in plants grown under GL (Su et al., 2014). The biochemical parameters which have been most strongly affected by GL (compared to RL or BL) and contribute to the impairment of plant

growth include lower chlorophyll content, reduced ribulose-1,5 bisphosphate carboxylase/oxygenase (Rubisco) activity and consequently, a decline in ETR and PSII efficiency (Landi et al., 2020).

In addition to this generalization, it is important to recognize that what is often described as a “monochromatic environment”, should more accurately be defined as a “narrowband light”, particularly for green light (GL). Indeed, supplementation with short- and long-wavelength GL may elicit different responses in plants (Dougher & Bugbee, 2007). Depending on the peak of the GL (usually ranging from 550 to 570), the absorbance by the inactive form of phytochrome (Pr) could be higher than that of Pfr. Therefore, the plant's responses may be derived from a trade-off between the effect of cryptochrome and phytochrome, which might explain why, in some cases, plants grown under green light have similar or even higher biomass yield (Pedroso et al., 2017; Amaki et al., 2011, respectively).

Biochemical modification triggered by GL also includes the secondary metabolism; for example, Adil et al. (2019) found that *W. somnifera* callus cultures grown in a monochromatic GL accumulated a higher withaferin A level than those grown with a cool white light, used as a control. Tariq et al. (2014) reported an increase in TPC and TFC, along with enhanced antioxidant activity in *A. absinthium* callus culture exposed to monochromatic GL compared to controls, i.e. callus culture grown in a cool white environment.

3 | SUPPLEMENTAL LIGHTING WITH TARGETED WAVEBANDS

If monochromatic environments are used to stimulate targeted secondary metabolisms or are relevant in a vertical farming context for short-term applications (i.e., spouts, microgreens), the supplementation of solar light with narrowband lamps represents a feasible technique in greenhouse cultivation to be applied transiently or during a whole cultivation cycle. Nowadays, LEDs are the leading source of light in agriculture. Compared to traditional lighting methods, LEDs have energy efficiency implications as they (1) have up to 2.5-fold longer life span than HPS lamps, (2) have low energy consumption due to the low heat emissions and (3) can be efficiently designed for controlling the light spectrum, the intensity and the scheduling to fine-tune their application based on the plant's needs (Bourget, 2008; Stamford et al., 2023).

In greenhouses, ML supplementation can increase the daylight intensity where daily light integral (DLI) is insufficient or extend the photoperiod by providing additional hours of illumination. The lighting enrichment by narrowband lamps can alter the spectral composition, capitalizing on the morphological, biochemical, and physiological responses connected with the exposure to specific monochromatic wavelengths. However, it is crucial to maintain a full-spectrum solar light background to ensure that plants receive all the necessary portions of the light spectrum. Selected wavebands can be applied individually or in combination, affecting plant productivity and morphology (Stamford et al., 2023). The consequences of light supplementation are not always consistent; in most cases, results are

genotype-dependent but also attributable to the DLI provided, as well as the season/latitude where light supplementation is employed.

The impacts of narrowband light supplementation on plant development, physiology, and biochemistry are summarised in Table 2. Effects which are not related to the alteration of light quality by narrowband lights (i.e., effects merely related to increased light flux) have been omitted. In all the studies reported in Table 2, narrowband lights provided by LED lamps were employed because of their advantages over older light sources (Morrow, 2008) and, generally, a maximum intensity of up to $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ was provided.

The supplementation of RL over sunlight increased plant productivity in strawberry (Lauria et al., 2023a) and mini cucumber ($>200 \mu\text{mol m}^{-2} \text{s}^{-1}$; de Freitas et al., 2021) but decreased the yield in sweet pepper (Kim & Son 2022) and tomato ($<100 \mu\text{mol m}^{-2} \text{s}^{-1}$; Kaiser et al., 2019). Similar results were observed when RL ($<100 \mu\text{mol m}^{-2} \text{s}^{-1}$) was added before or after natural light exposure, resulting in increased strawberry fruit production (Choi et al., 2015) and plant development in cucumber and tomato (Wang et al., 2021, 2022, respectively). Despite the positive results observed in terms of productivity, supplemental RL often decreased net photosynthesis, reduced stomatal size, lowered Rubisco activity and decreased carbon export from the Calvin-Benson cycle in tomato (Kaiser et al., 2019), strawberry (Lauria et al., 2021, 2023c), and basil plants (Jensen et al., 2018; Lauria et al., 2023b). This reduction was associated with decreased PSII efficiency and PSII antenna's ability for energy conservation (Kaiser et al., 2019; Lauria et al., 2023c). Moreover, RL also led to a reduction in abscisic acid content in basil (Jensen et al., 2018). This behaviour could be partially explained by alterations in the expression of both PSII and PSI multiprotein complexes (Muneer et al., 2014). In contrast, when RL enrichment is applied in artificial lighting instead of over a natural background, even when RL is predominant, the observed effects are usually positive and consistent across different crops. In fact, it has been reported that a 2:1 to 4:1 red-to-blue (RL:BL) ratio, irrespectively of the fluence, enhances photosynthetic performances and increased net photosynthesis, transpiration rates and stomatal conductance in cucumber (Wang et al., 2021), mini cucumber (de Freitas et al., 2021), tomato (Wang et al., 2022; Zhang et al., 2022b) and *Impatiens hybrida* (Kobori et al., 2022).

Besides physiological effects, RL supplementation can also affect primary and secondary metabolism. Lower intensities of RL increased starch and sucrose (tomato; $125 \mu\text{mol m}^{-2} \text{s}^{-1}$; Zhang et al., 2022b) as well as glucose and fructose (sweet pepper; $71 \mu\text{mol m}^{-2} \text{s}^{-1}$; Kim & Son, 2022). These alterations could be related to the modulation of carbohydrate metabolism by phytochrome A and B (PHYA and PHYB), with PHYA promoting starch accumulation under a wide range of light conditions through a signalling cascade involving the plastidial nucleoside diphosphate kinase-2 (NDPK2) and glucose-1-phosphate adenyltransferase small subunit (APS1) (Han et al., 2017). Conversely, Lauria et al. (2023a) observed that higher intensities ($250 \mu\text{mol m}^{-2} \text{s}^{-1}$) of RL led to a reduction of sugars and organic acids content in strawberry fruits, suggesting that RL irradiation might accelerate glycolysis and tricarboxylic acid (TCA) cycle.

Regarding changes in secondary metabolism, supplemental RL has been shown to promote the accumulation of compounds belonging to different classes, including quercetin (*I. hybrida* cv. White; Kobori et al., 2022), ascorbic acid, carotenoids (sweet pepper; Kim & Son, 2022), anthocyanins (strawberry fruits; Lauria et al., 2023a), and xanthophylls (strawberry leaves; Lauria et al., 2021). After cold storage, tomato fruit treated with a pre-harvest ratio of 3:1 RL:BL showed increased lycopene and carotene contents (Appolloni et al., 2023). When RL was exclusively used to extend the photoperiod, an increase in chlorophyll content was reported in strawberry leaves and tomatoes (Choi et al., 2015, Wang et al., 2022, respectively), along with elevated carotenoid content in cucumber and tomatoes (Wang et al., 2021, 2022, respectively), higher carbohydrate levels in rocket salad (Sarabi et al., 2022), increased sugar content in strawberry fruit, cucumbers and tomatoes (Choi et al., 2015, Wang et al., 2021, 2022, respectively), and elevated flavonoid and tannin contents in rocket salad (Sarabi et al., 2022). Choi et al. (2015) also reported an increase in oxalic and malic acids, anthocyanins, and antioxidant activity in strawberry fruit, while Sarabi et al. (2022) noted a decrease in nitrate content and NH_4^+ in *Eruca sativa* due to increased glutamine synthetase activity, which catalysed the conversion of NH_4^+ into glutamine.

Although FR light is usually considered marginally in greenhouse cultivation, with a high R:FR ratio generally preferred (see section 3), some studies have reported impacts of supplemental FR light on the physiology, morpho-anatomy and both primary and secondary metabolisms of plants, for example, increased plant height (*Taxus baccata*; Chiochio et al., 2022) and improved post-harvest cold tolerance in tomatoes (Affandi et al., 2020). When added to a background of supplemental wide-spectrum light, FR light increased the maximum quantum yield of PSII photochemistry, both in conditions of high and low R:FR ratio (Matysiak, 2021). Additionally, FR light supplementation promoted the accumulation of sucrose, glucose, fructose, and ascorbic acid in sweet pepper (Kim & Son, 2022).

A large body of experimental work explored the effect of supplemental BL on biomass, morpho-anatomical, and physiological responses, as well as its impact on both primary and secondary plant metabolism. The addition of 25–30% B light (approximately $100 \mu\text{mol m}^{-2} \text{s}^{-1}$) led to a reduction in triose phosphate use but correlates with an increase in photosynthetic capacity, quantum yield for CO_2 assimilation, and rates of daytime respiration in tomato (Kaiser et al., 2019, Kalaitzoglou et al., 2021). In cucumber, the supplementation with $180 \mu\text{mol m}^{-2} \text{s}^{-1}$ of BL increased net photosynthesis and transpiration rates (Yan et al., 2022). These improvements were likely caused by the enhancement in the activity/expression of key components of the photosynthetic process, such as Rubisco, cytochrome f complexes, chlorophylls, and light harvesting complexes proteins of PSII (Matsuda et al., 2004). Conversely, the application of higher intensity of BL ($250 \mu\text{mol m}^{-2} \text{s}^{-1}$) might exert a detrimental effect on photosynthetic activity (strawberry; Lauria et al., 2021). This effect likely stemmed from BL influences on leaf physiology, possibly through the impact on chloroplast movement, as well a reduction in carbonic anhydrase activity (Momayyezi & Guy, 2017), which might explain the decrease in plant biomass and leaf area observed in some

TABLE 2 Effects of narrowband light supplementation on plant development, physiology, and biochemistry during daylight, as additional light hours or during nighttime. A – CO₂ net assimilation rate; ABA – abscisic acid; ABA-GE – abscisic acid glucosylester; B – blue light; Ci – intercellular CO₂ concentration; DEPS – de-epoxidation state of xanthophylls cycle pigments; DPPH – 2,2-diphenyl-1-picrylhydrazyl radical scavenging rate; E – transpiration rate; ETR – electron transport rate; FR – far red light; FRAP – ferric-reducing antioxidant power; Fv/Fm – maximum quantum yield of PSII; Fv'/Fm' – efficiency of excitation energy captured by open PSII reaction centers; G – green light; gm – mesophyll conductance; gs – stomatal conductance; GS – glutamine synthetase; J₁₃₀₀ – electron transport obtained at saturating light; NiR – nitrite reductase; O – orange light; Pl_{abs} – performance index for energy conservation from photons absorbed by PSII antenna, to the reduction of Q_B; Pn – net photosynthetic rate; qN – non-photochemical quenching coefficient; R – red light; TPU – triose phosphate utilisation; VAZ – total amount of xanthophyll cycle components; Vcmax – maximum rate of carboxylation of Rubisco; W – white light; WUE – water use efficiency; Y – yellow light; ΦPSI – quantum yield of PSI; ΦPSII – quantum yield of PSII; ΦNPQ – quantum yield of regulated non-photochemical energy loss in PSII; φ_{Eo} – quantum yield of the electron transport flux from Q_A to Q_B; ψ₀ – efficiency with which a trapped exciton can move an electron further than Q_A⁻ into the electron transport chain.

Daylight supplemental irradiances					
Species	Light recipe	Intensity	Duration	Effects	Reference
<i>Solanum lycopersicum</i>	R + 0, 6, 12, 24% B	99 μmol·m ⁻² s ⁻¹	Photoperiod 16 h for 111 days	R ↑ plant height, leaf area, rates of day respiration; ↓ biomass, Fv/Fm, TPU. R + 24B ↑ photosynthetic capacity, rate of day respiration; ↓ biomass, leaf area, stem length, TPU	Kaiser et al. (2019)
	FR	30 or 50 μmol·m ⁻² s ⁻¹	Photoperiod 16 h long term	FR ↓ weight loss, pitting, softening in mature green tomatoes; ↑ firmness, ↓ weight loss and decay during shelf-life in red tomatoes	Affandi et al. (2020)
	B (increasing percentage up to 61%)	100 μmol·m ⁻² s ⁻¹	Photoperiod 16 h for 30 days	Increasing B ↑ ΦPSI; ↓ leaf area, height, biomass	Kalaitzoglou et al. (2021)
	B (supplied intermittently)	100 μmol·m ⁻² s ⁻¹	Photoperiod 12 h for 46 days	↑ earlier flowering, ethylene, lycopene, phenolics and flavonoids, DPPH, FRAP, free amino acids, soluble sugars, vitamin C	He et al. (2022)
	WR, 2R:1B	125 μmol·m ⁻² s ⁻¹	Photoperiod 8 h for 30 days	WR ↑ plant height, total leaf area, root length, root volume, root activity, photosynthetic parameters, starch and sucrose content; ↓ hypocotyl length. RB ↑ stem diameter, sucrose content; ↓ hypocotyl length	Zhang et al. (2022b)
	3R:1B	180 μmol·m ⁻² s ⁻¹	Photoperiod 16 h for 60 days	↑ lycopene and β-carotene after cold storage	Appolloni et al. (2023)
<i>Cucumis sativus</i> (hybrid Larino)	4R:1B	220 μmol m ⁻² s ⁻¹	Photoperiod 12 h for about 120 days	↑ A, WUE and E, cucumber yield, precocity; ↓ fruit curve	de Freitas et al. (2021)
<i>Ocimum basilicum</i> (green-leafed basil)	B	300 μmol m ⁻² s ⁻¹	Photoperiod 16 h up to 48 days	B ↑ cichoric acid and quercetin rhamnoside	Taulavuori et al. (2016)
	4R:1B, 4R:1B + UVA, 2R:3B, 4R:1G	120 μmol m ⁻² s ⁻¹	Photoperiod 20 h for 28 days	2R:3B ↑ Leaf Mass Area, leaf dry weight, abaxial stomatal density; ↓ Specific Leaf Area compared to 4R:1B. 4R:1G ↓ adaxial stomatal size, adaxial pore area, gs, ABA and ABA-GE	Jensen et al. (2018)
	W, B, R	130 μmol m ⁻² s ⁻¹	Photoperiod 16fh. for 45 days	B ↑ flavonol biosynthesis; ↓ stem length	Matysiak and Kowalski (2019)
	W (R:G:B, 1:1:1), G, B, R	250 μmol m ⁻² s ⁻¹	5 h d ⁻¹ from 11 a.m. to 4 p.m. for 21 days	W ↑ n° stomata, gs, Ci, caftaric acid, rutin; ↓ WUE. G ↑ n° stomata, WUE, caffeic and caftaric acid; ↓ leaf area, gs, Ci, ΦPSII. B ↑ n° stomata, gs, Ci, ETR, ΦPSII, caffeic and caftaric acid, rutin; ↓ leaf area, WUE, ΦNPQ. R ↑ Ci, ↓ Pn, WUE	Lauria et al. (2023b)

(Continues)

TABLE 2 (Continued)

Daylight supplemental irradiances					
Species	Light recipe	Intensity	Duration	Effects	Reference
<i>Ocimum basilicum</i> (red-leafed basil)	W, B, R	130 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h for 45 days	W \uparrow plant height, leaf number and leaf size. B \uparrow flavonol biosynthesis	Matysiak and Kowalski (2019)
		250 $\mu\text{mol m}^{-2} \text{s}^{-1}$	5 h d^{-1} from 11 a.m. to 4 p.m. for 21 days	W \downarrow WUE. G \uparrow n $^\circ$ stomata, WUE, flavonol; \downarrow Pn, gs, Ci, caffeic acid, Cy-3-coum-Glc. B \uparrow n $^\circ$ stomata, gs, flavonols, anthocyanins, caftaric acid; \downarrow WUE, Φ PSII. R \downarrow n $^\circ$ stomata, Φ PSII, caffeic acid	Lauria et al. (2023b)
<i>Capsicum annuum</i>	4R:1B, 4R:1B + FR	71 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (+ 55 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for FR)	Photoperiod 12 h for 30 days	4R:1B \uparrow sucrose, glucose, fructose, ascorbic acid, carotenoid; \downarrow fruit weight, number of fruit. 4R:1B + FR \uparrow yield, fruit lengths and widths, sucrose, glucose, fructose, ascorbic acid	Kim and Son (2022)
<i>Fragaria</i> \times <i>ananassa</i>	W (R:G:B, 1:1:1), G, B, R	250 $\mu\text{mol m}^{-2} \text{s}^{-1}$	5 h d^{-1} from 11 a.m. to 4 p.m. for 17 days	After 1 day: W \uparrow qN, DEPS, superoxide anion R \uparrow chlorophylls, DEPS, superoxide anion. B \uparrow qN, DEPS. G \uparrow qN, VAZ, DEPS. After 17 days: W \uparrow Pn, gs, gm, superoxide anion. R \downarrow Pn, gm, Vcmax, J1300, TPU, qN, chlorophylls, \uparrow VAZ, superoxide anion. B \uparrow superoxide anion; \downarrow Pn, gs, gm, Vcmax, J ₁₃₀₀ , TPU. G \uparrow VAZ; \downarrow qN	Lauria et al. (2021)
	W (R:G:B, 1:1:1), G, B, R	250 $\mu\text{mol m}^{-2} \text{s}^{-1}$	5 h d^{-1} from 11 a.m. to 4 p.m. for about 90 days	G \uparrow primary metabolites, phenolics. B \uparrow primary metabolites, phenolics. R \uparrow plant productivity, anthocyanins, expression of genes related to the cell wall defence; \downarrow primary metabolites	Lauria et al. (2023a)
	W (R:G:B, 1:1:1), G, B, R	250 $\mu\text{mol m}^{-2} \text{s}^{-1}$	5 h d^{-1} from 11 a.m. to 4 p.m. for 60 days	R \uparrow maximum trapped exciton flux per PSII, H ₂ O ₂ , MDA, SOD APX; \downarrow petiole length, P _n , PI _{abs} , Ψ_0 , Φ_{E0} , carotenoids, α -tocopherol. B \uparrow MDA, SOD, APX; \downarrow petiole length, biomass, leaf area, carotenoid, α -tocopherol, H ₂ O ₂ . G \downarrow petiole length, biomass, leaf area, PI _{abs} , H ₂ O ₂ . W \uparrow MDA; \downarrow biomass, leaf area.	Lauria et al. (2023c)
<i>Valerianella locusta</i>	W, B, R	130 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h for 30 days	W \uparrow plant height, leaf number, leaf size. B \uparrow flavonol biosynthesis	Matysiak and Kowalski (2019)
<i>Eruca sativa</i>	W, B, R	130 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h for 30 days	W \uparrow plant height, leaf number, leaf size. B \uparrow flavonol biosynthesis	Matysiak and Kowalski (2019)
<i>Lactuca sativa</i> var. Lollo rossa	B	300 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 16 h up to 48 days	B \uparrow quercetin-malonyl diglucoside, quercetin 3-malonylglycoside, chicoric acid; \downarrow protocatechuic acid	Taulavuori et al. (2016)
<i>Taxus baccata</i>	B, R, 2R:1B + FR	100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (R, B). 50, 100, 150 $\mu\text{mol m}^{-2} \text{s}^{-2}$ (2R:1B + FR)	Photoperiod 14 h for 120 days	2R:1B + FR \uparrow plant height	Chiocchio et al. (2022)
<i>Impatiens hybrida</i> hort cv. 'Royal Magenta' and cv. 'White'	83R:17B, 3R:1B, 67R:33B, 2R:1R1:1B	150 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 12 h for 210 days	White cv: R83:B17 \uparrow trichomes, plugs compaction. 3R:1B \uparrow cuttings. R67:B33 \uparrow cuttings, quercetin, trichomes. Royal Magenta cv: R83:B17 \downarrow oxidative	Kobori et al. (2022)

TABLE 2 (Continued)

Daylight supplemental irradiances					
Species	Light recipe	Intensity	Duration	Effects	Reference
<i>Rosa × hybrida</i>	R, B, W, RBW + FR (high R:FR ratio), RBW + FR (low R:FR ratio)	200 $\mu\text{mol m}^{-2} \text{s}^{-1}$	Photoperiod 18 h for 42 days	damage; \uparrow trichomes. 3R:1B \uparrow photosynthesis; \downarrow oxidative damage. R67:B33 \uparrow photosynthesis, trichomes R \uparrow n° of shoots per plant. RBW + FR (both high and low R:FR ratio) \uparrow Fv/Fm	Matysiak (2021)
Additional hours					
<i>Fragaria × ananassa</i>	B, R, 7R:3B	75 $\mu\text{mol m}^{-2} \text{s}^{-1}$	6 h for \approx 170 days	R \uparrow petioles, chlorophyll, oxalic and malic acid, total phenolic compounds, antioxidant activity. B \uparrow length of leaflets, fruit production, anthocyanins. 7R:3B \uparrow petioles, length of petioles, width of leaflets, fruit production, chlorophyll, fructose, anthocyanins	Choi et al. (2015)
<i>Anoectochilus roxburghi</i>	R, B, Y, G, W	30 $\mu\text{mol m}^{-2} \text{s}^{-1}$	3 h for 40 days	R \uparrow root length, qN; \downarrow Chl a fluorescence yield. B \uparrow leaf number, stem diameter, root length, fresh and dry weight, Chlorophyll a, total flavonoids, total polyphenol; \downarrow soluble proteins. Y \uparrow root length, Chlorophyll a fluorescence yield, soluble sugars, polysaccharides, stomatal density, root vitality. G \uparrow qN; \downarrow total polyphenols. W \uparrow qN; \downarrow soluble and reducing sugars	Wang et al. (2018)
<i>Cucumis sativus</i>	7R:2B	Nd	1, 2 or 3 h for 30 days	\uparrow plant growth, root development and vigour, root dry matter accumulation, net photosynthetic rate, transpiration rate, stomatal conductance, chlorophylls and carotenoids, Fv/Fm, ΦPSII , qP, Fv'/Fm', Calvin Cycle enzyme activity, phosphate synthase, acid invertase, neutral invertase, sucrose, fructose, and glucose; \downarrow Ci	Wang et al. (2021)
<i>Solanum lycopersicum</i>	7R:2B	51 $\mu\text{mol m}^{-2} \text{s}^{-1}$	3 h in the morning or in the evening for 30 days	In the morning \uparrow dry matter accumulation, root growth, height, leaf area, gas exchange parameters, photosynthetic capacity, Rubisco enzyme activity, photosynthetic products, chlorophylls, carotenoids. In the evening \uparrow stem diameter, height, leaf area, gas exchange parameters, photosynthetic capacity, Rubisco enzyme activity, photosynthetic products	Wang et al. (2022)
<i>Eruca sativa</i>	R, B, 75R:25B, 25R:75B, 50R:50B, W	200 $\mu\text{mol m}^{-2} \text{s}^{-1}$	6 h for 28 days	R \uparrow GS activity; \downarrow NH_4^+ . B \uparrow vitamin C, GS activity, NiR activity; \downarrow nitrate content, NH_4^+ . 3R:1B \uparrow carbohydrates, flavonoids, tannins, GS activity, amino acids; \downarrow nitrate content, NH_4^+ . 1R:3B \uparrow GS activity NiR activity; \downarrow NH_4^+ . 1R:1B \uparrow carbohydrates, phenols, flavonoids, tannins, GS activity, amino acids; \downarrow nitrate content, NH_4^+ . W \downarrow NH_4^+	Sarabi et al. (2022)

(Continues)

TABLE 2 (Continued)

Daylight supplemental irradiances					
Species	Light recipe	Intensity	Duration	Effects	Reference
Night supplementation					
<i>Fragaria</i> × <i>ananas</i>	B, G, R	80 $\mu\text{mol m}^{-2} \text{s}^{-1}$	16 h for 356 days	B ↑ number of florets and flower cluster per plant, fresh weight of flower cluster. R ↓ number of florets and flower cluster per plant	Magar et al. (2018)
<i>Lactuca sativa</i> cv. 'Red Mist'	W, 57R:43B, and B/UVA	167 $\mu\text{mol m}^{-2} \text{s}^{-1}$	12 h for 3 days	All treatments ↑ dry weight, carotenoids, total phenol content, trolox equivalent antioxidant capacity; ↓ specific leaf area. RB ↑ SPAD. W ↑ SPAD	Hooks et al. (2022)

species (tomato; Kaiser et al., 2019; Kalaitzoglou et al., 2021; basil; Matysiak & Kowalski, 2019; Lauria et al., 2023b). Of note, BL has been reported to be more effective at opening stomata than RL (Violet-Chabrand et al., 2021), which involves the release of stored energy and osmolytes from starch degradation or lipid metabolism (Horner et al., 2016). As a consequence, BL resulted in greater stomatal conductance and transpiration rates in both green- and red-leafed basil (Jensen et al., 2018; Lauria et al., 2023b). However, BL-induced stomatal opening does not necessarily rely on higher photosynthesis, suggesting that the guard cell mitochondria play a key role in powering the BL response and that species-specific BL-induced stomatal, in terms of both rapidity and magnitude, must be considered (Violet-Chabrand et al., 2021).

Supplemental BL ($250 \mu\text{mol m}^{-2} \text{s}^{-1}$) also increased primary metabolite content in strawberry fruit, mainly organic acids, sugars, and amino acids (Lauria et al., 2023a) and promoted changes to the secondary metabolism, such as increasing flavonoid content in a *plethora* of species including green basil (Taulavuori et al., 2016; Matysiak & Kowalski, 2019; Lauria et al., 2023b) red-leafed sweet basil (Matysiak & Kowalski, 2019; Lauria et al., 2023b), lamb's lettuce and garden rocket (Matysiak & Kowalski, 2019), red-leafed lettuce (Taulavuori et al., 2016), and tomato (He et al., 2022). BL also promoted the accumulation of phenolic content in red-leafed lettuce, tomato and strawberry (Taulavuori et al., 2016, He et al., 2022, Lauria et al., 2023a, respectively) as well as anthocyanins in red-leafed basil (Lauria et al., 2023b). Indeed, BL has been shown to overexpress the transcript levels of genes encoding PAL and flavonoid-3'-hydroxylase, with the former playing a key role in flavonoid biosynthesis by channelling primary metabolites into this secondary pathway (Thwe et al., 2014). In other cases, BL was also reported to increase antioxidative capacity, level of lycopene, vitamin C, free amino acids, and soluble sugars (e.g. tomato; He et al., 2022) and promote the decrease in nitrate and NH_4^+ , likely due to the stimulated activity of nitrate metabolism enzymes (*E. sativa*; Sarabi et al., 2022).

To date, little research has explored the impact of supplementing GL in the greenhouse environment. Despite an increase in stomatal number, supplemental GL led to a decrease in stomatal conductance and, consequently, in internal CO_2 concentration in both green- and red-leafed basil, thereby positively influencing water use efficiency (Lauria

et al., 2023b). Regarding secondary metabolism changes, some studies have reported that GL increases xanthophyll content at high intensities after a single day of supplementation (strawberry leaves; Lauria et al., 2021), increases primary metabolites and phenolics in strawberry fruit (Lauria et al., 2023a), and enhances the flavonoid metabolism in red-leafed basil after long-term treatment (Lauria et al., 2023b). However, the few studies on the effect of supplemental GL on secondary metabolism make it challenging to draw general conclusions.

In addition to the aspects mentioned above, recent experiments have also explored the possibilities of supplementing additional hours of narrowband light during the night. Supplemental hours of both BL and yellow (Y) light during nighttime showed positive effects in terms of biomass, photosynthesis, and secondary metabolite production in *Anoectochilus roxburghii*, while RL, GL, and white light decreased secondary metabolite content ($30 \mu\text{mol m}^{-2} \text{s}^{-1}$; Wang et al., 2018). Similarly, in strawberry plantlets, additional hours of BL during the night positively affect flowering and biomass, while R light revealed the opposite effect (Magar et al., 2018). The authors hypothesize that a BL increase in the cytokinin levels stimulates flowering, while the inhibition of this process was potentially connected with the RL activation of endogenous gibberellins. Moreover, Lin (2000) reported the control of flower induction genes (i.e., FLOWER LOCUS T and SUPPRESSOR OF OVEREXPRESSION OF CONSTANS1) by cryptochrome and phytochrome in *Arabidopsis*. Further investigations may shed light on whether night supplementation can represent a feasible greenhouse technique for improving the quality of horticultural crops. If it is proven to offer benefits in terms of yields or nutraceutical properties, it could potentially replace daytime light supplementation, thereby reducing lamp energy costs.

4 | LIGHT MODULATION THROUGH COVERING MATERIALS

Among all the covering materials used in agriculture, those able to modulate the light spectrum and covered to some extent in literature are (1) films which can exclude specific undesirable wavebands, (2) photo-selective coloured shading nets and films which can considerably modify the full light spectrum, (3) photo-converting films with

TABLE 3 Effects of light-exclusion films on ornamental and horticultural species. B – blue light; FR – far-red light; R – red light; UV – ultra-violet light.

Excluded light	Species	Effects	Reference	
R	<i>Cosmos bipinnatus</i>	↓ shoot dry weight	Cerny et al. (2003)	
	<i>Dendranthema × grandiflorum</i>	↑ stem elongation in chrysanthemum, ↓ shoot dry weight ↑ height, internode length	Cerny et al. (2003) Khattak and Pearson (2006)	
	<i>Eustoma grandiflorum</i>	↑ height. No effects on dry weight. No effects on days to flower or bud number	Wilson and Rajapakse (2001a)	
	<i>Pachystachys lutea</i>	↑ height	Wilson and Rajapakse (2001b)	
	<i>Zinnia elegans</i>	↓ shoot dry weight	Cerny et al. (2003)	
FR	<i>Antirrhinum majus</i>	↓ shoot dry weight. Delaying in anthesis ↓ extension growth in all species both for continuative exposition and for a short time exposition. Delaying in flowering	Cerny et al. (2003) Runkle and Heins (2002)	
	<i>Capsicum annum</i>	↓ height, total leaf area, leaf size. Number of leaves was not affected	Li et al. (2000)	
	<i>Cosmos bipinnatus</i>	↓ height, shoot dry weight	Cerny et al. (2003)	
	<i>Dendranthema × grandiflorum</i>	↓ height, total leaf area, leaf size. Number of leaves was not affected. ↓ height especially in the early vegetative period, flower dimension. Far-red filters did not affect anthesis ↓ height, shoot dry weight. Delaying in anthesis	Li et al. (2000) Li et al. (2003a) Cerny et al. (2003)	
	<i>Euphorbia pulcherrima</i>	↓ plant height. Delaying in flower induction	Clifford et al. (2004)	
	<i>Eustoma grandiflorum</i>	↓ height, stem dry weight. No effects on days to flower or bud number	Wilson and Rajapakse (2001a)	
	<i>Impatiens walleriana</i>	↓ height ↓ extension growth in all species both for continuative exposition and for a short time exposition	Fletcher et al. (2005) Runkle and Heins (2002)	
	<i>Lactuca sativa var. crispata</i>	↑ calcium content, ↓ dry matter, chlorophyll. The incidence of tip-burned leaves decreased. No effects on yield	Kleemann (2002)	
	<i>Orthosiphon stamineus</i>	↓ height, leaf area, leaf and stem dry weight	Wilson and Rajapakse (2001b)	
	<i>Pachystachys lutea</i>	↓ height, leaf and stem dry weight	Wilson and Rajapakse (2001b)	
	<i>Petunia × hybrida</i>	↓ shoot dry weight. Delaying in anthesis ↓ extension growth in all species both for continuative exposition and for a short time exposition. Delaying in flowering ↓ height. Flowering was delayed under lower PAR-transmission films	Cerny et al. (2003) Runkle and Heins (2002) Fletcher et al. (2005)	
	<i>Salvia × 'Indigo Spires', Salvia splendens 'Van Houttei', and Salvia leucantha</i>	↓ height, greenness (only in 'Indigo Spires'), stem dry weight. ↑ greenness (only in 'Van Houttei')	Wilson and Rajapakse (2001c)	
	<i>Solanum lycopersicon</i>	↓ extension growth in all species both for continuative exposition and for a short time exposition	Runkle and Heins (2002)	
	<i>Strobilanthes dyerianus</i>	↓ leaf and stem dry weight	Wilson and Rajapakse (2001b)	
	<i>Viola × wittrockiana</i>	↓ extension growth in all species both for continuative exposition and for a short time exposition. Delaying in flowering	Runkle and Heins (2002)	
	<i>Zinnia elegans</i>	↓ height, shoot dry weight. Delaying in anthesis	Cerny et al. (2003)	
	R + FR	<i>Gardenia jasminoides</i>	↓ height, leaf area of cuttings and plants, number of nodes, shoot fresh and dry weight. No lateral shoot development ↓ height, leaf area in cuttings, fresh and dry weight in plants rooted and grown under the film, lateral shoot if rooted under control and then moved under photo-selective film	Lykas et al. (2005) Lykas et al. (2008)
		<i>Dendranthema × grandiflorum</i>	↓ height, internode length, time to flowering, leaf area, leaf size, fresh and dry weight	Khattak and Pearson (2006)

(Continues)

TABLE 3 (Continued)

Excluded light	Species	Effects	Reference
UV	<i>Brassica oleracea</i>	↑ compactness	Stapel et al. (2011)
	<i>Cucumis sativus</i>	↑ compactness	Stapel et al. (2011)
	<i>Gazania rigens</i>	↑ compactness	Stapel et al. (2011)
	<i>Lactuca sativa</i> cv Lollo Rosso	UV filters ↓ secondary metabolites, photosynthetic efficiency, ↑ growth. UV transparent films ↑ anthocyanin, flavonoid and phenolic content	Tsormpatsidis et al. (2008)
	<i>Solanum lycopersicon</i>	↑ compactness	Stapel et al. (2011)
	<i>Solanum melongena</i>	No effects on fruit quality characteristics, nutritional value, and organoleptic properties	Papaioannou et al. (2012)
		↑ plant height, leaf length, leaf width, chroma parameter, production quantity and quality	Kittas et al. (2006)

fluorescent dyes and the ability to induce a photonic shift toward more desirable wavebands, (4) and light-diffusing plastic films which can alter light distribution inside the greenhouses (Figure 3). Lastly, plants can also be influenced by light modification induced by coloured mulching films, which can alter the reflectance of the light spectrum.

4.1 | Light-exclusion films

The investigation into the possibility of modulating solar light spectra started mostly at the beginning of this century, and for this purpose, photo-selective plastic films emerged as a promising and widespread solution. They generated significant interest, especially within the floricultural sector, where the requirement to minimize the use of chemical products to control plant size, shape and development has become increasingly urgent.

Notably, light perception by photoreceptors resulted in a key process for the regulation of a plethora of physiological mechanisms. For example, chemical plant growth regulators (PGRs), commonly employed in the floricultural sector, act as anti-gibberellins, leading to a reduction in plant growth (Maki et al., 2002). However, hormones like gibberellic acid (GA) or ABA are originally mediated by phytochromes and can consequently be regulated through the manipulation of the light spectrum, particularly the R:FR ratio (Seo et al., 2006). Moreover, phytochromes regulate a wide variety of processes involving all stages of plant development, including seed germination, flowering time, fruit quality, root elongation and, partially, shade avoidance syndrome (Strasser et al., 2010; Casal et al., 2012; González et al., 2015).

Indeed, the use of R selective plastic films established a low R:FR ratio that may naturally occur following inter-plant canopy shading under high plant density conditions. This reduction in the R:FR ratio can lead to several undesirable consequences in ornamental plant development, including excessive stem elongation and internode extension in *Dendranthema × grandiflorum* (Cerny et al., 2003; Khattak & Pearson, 2006), *Eustoma grandiflorum* (Wilson & Rajapakse, 2001a), *Euphorbia pulcherrima* (Clifford et al., 2004) and *Pachystachys lutea* (Wilson & Rajapakse, 2001b).

It also decreased plant dry weight in *Cosmos bipinnatus*, *D. × grandiflorum*, *Zinnia elegans* (Cerny et al., 2003), and *Salvia* spp. (Wilson & Rajapakse, 2001c) while decreasing axillary branching in *E. pulcherrima* (Clifford et al., 2004).

On the contrary, the depletion of FR light due to the employment of photo-selective plastic films leads to an increase in the R:FR ratio leading to more compact plant structures due to a reduced internode length and decrease in plant dry weight in many ornamental and horticultural species such as *Antirrhinum majus* (Runkle & Heins, 2002; Cerny et al., 2003), *Capsicum annuum* (Li et al., 2000), *C. bipinnatus* and *Z. elegans* (Cerny et al., 2003), *D. grandiflorum* (Li et al., 2000; Li et al., 2003a; Cerny et al., 2003), *E. pulcherrima* (Clifford et al., 2004), *E. grandiflorum* (Wilson & Rajapakse, 2001a), *Gardenia jasminoides* (Lykas et al., 2005, 2008), *Gazania rigens*, *B. oleracea*, *Cucumis sativus* and *Solanum lycopersicum* (Stapel et al., 2011), *Impatiens walleriana* and *Viola × wittrockiana* (Runkle & Heins, 2002), *L. sativa* (Kleemann, 2002), *Orthosiphon stamineus*, *P. lutea* and *Stobilanthes dyerianus* (Wilson & Rajapakse, 2001b), *Petunia × hybrida* (Cerny et al., 2003; Runkle & Heins, 2002; Fletcher et al., 2005), several *Salvia* species (Wilson & Rajapakse, 2001c). Furthermore, FR light can affect the timing of anthesis, generally delaying flowering in long-day plants as such *Z. elegans* and *D. × grandiflorum* (Cerny et al., 2003), *A. majus* (Runkle & Heins, 2002; Cerny et al., 2003), *P. × hybrida* (Runkle & Heins, 2002; Cerny et al., 2003; Fletcher et al., 2005) and *E. pulcherrima* (Clifford et al., 2004). This side effect can be avoided by exposing plants to an FR-deficient environment during the vegetative stage or ensuring high PAR transmission under the photo-selective film, thereby allowing for rapid anthesis (Runkle & Heins, 2002; Fletcher et al., 2005). Other effects induced by a FR-deficient environment include a decreased leaf area in cuttings and plants such as *C. annuum* and *D. × grandiflorum* (Li et al., 2000), and *G. jasminoides*, (Lykas et al., 2005, 2008), inhibition of lateral shoot development in *G. jasminoides*, (Lykas et al., 2008), reduced leaf size in *D. × grandiflorum* and *C. annuum* (Li et al., 2000), and a decrease in chlorophyll content in *L. sativa* (Kleemann et al., 2004).

On the other hand, B absorbing films did not alter phytochrome photo-equilibrium significantly and only slightly changed the R:FR

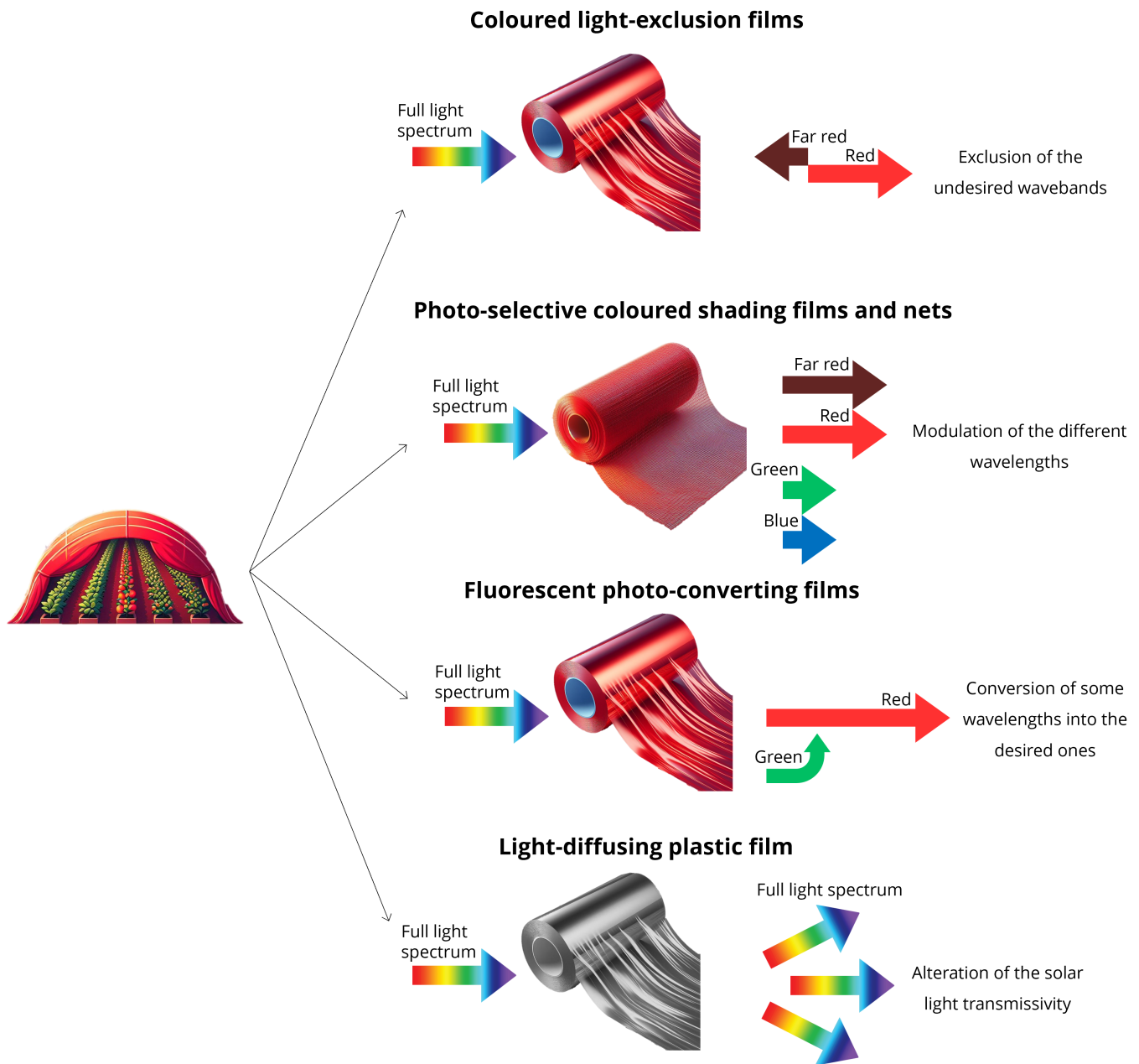


FIGURE 3 Light modulations obtained through the application of covering materials, using red color only as an example. A broader framework of the effects induced by these covering materials and their different colors and properties is extensively reported in Table 3 (light-exclusion films), Table 4 (photo-selective shading nets), Table 5 (fluorescent photo-converting films) and Table 6 (light-diffusing plastic films).

ratio, which led to reduced plant height, shorter internode lengths, accelerated time to flowering, and reduced leaf area, and leaf size, as well as fresh and dry weight in *D. grandiflorum* (Khattak & Pearson, 2006). These effects observed in the absence of BL provide evidence for a connection between BL and phytochrome-mediated light perception. When phytochrome activity is lower, BL can promote plant elongation to a greater extent than R light (Kong et al., 2018).

Greenhouse covers can also differ in their UV-blocking properties, affecting crops differently. According to the Planck equation, UV photons (at 390 nm, minimum energy for UV) count for more than 80% more energy than R photons (at 700 nm), though high-energy photons

are not fully exploited for photosynthesis due to inherent photochemical inefficiencies (Long et al., 2006). UV-transmitting films increased anthocyanin, flavonoid, and phenolic content in red *L. sativa* and *Vitis vinifera* (Tsormpatsidis et al., 2008; Marigliano et al., 2022, respectively). These films also led to increased compactness in different ornamental and horticultural plants such as *G. rigens*, cabbage, cucumber, and tomato (Stapel et al., 2011). In contrast, UV-blocking coverings decreased secondary metabolite accumulation and photosynthetic efficiency in red *L. sativa* but assured an increased growth and better quality in red *L. sativa* and *Solanum melongena*. This effect is particularly evident when utilizing materials with 0% UV

transmission, which enhance the chroma parameter akin to colour intensity or saturation. This enhancement likely occurs through alterations in the flavonoid composition. (Kittas et al., 2006; Tsormpatzidis et al., 2008). Additionally, UV-blocking films serve as valid tools for pest management (Doukas & Payne, 2014; Papaioannou et al., 2012; Chi et al., 2019; Wang et al., 2023). However, it is worth noting that in tomato (cv. 'Belladonna') the lycopene and ascorbic acid content were similar when grown under low-density polyethylene and UV-absorbing polyethylene greenhouse covering films, despite differences in UV transmittance between the treatments (Papaioannou et al., 2012).

4.2 | Photo-selective coloured shading films and nets

More recently, coloured shading nets and films have emerged on the market, offering enhanced shading properties. These coloured photo-selective nets are typically made of polypropylene or polyethylene, knitted with different mesh sizes to achieve the desired level of shading. They contain different chromophores that enable the nets to filter specific solar wavebands and scatter light (Zoratti et al., 2015; Manja & Aoun, 2019). Therefore, these nets not only enable light depletion but also bring about a complex alteration in the spectrum of light. This results in improvements in horticultural product quality, protection against unfavourable weather conditions, and a reduction in physiological disorders and flower abortion (Stagnari et al., 2018). The effects of coloured shading films and nets on horticultural species are summarised in Table 4.

R photo-selective films and nets enhance R and FR transmittance while absorbing UV, B, and G lights. Under these coverings, the R:FR ratio and phytochrome photo-equilibrium are generally unaffected. However, their influence on plant morphogenesis and specific physiological and biochemical parameters has been recorded. Under these nets, higher dry weights of both the plant and fruit of *Vanilla planifolia* (Sanchez et al., 2022) and *Actinidia deliciosa* (Basile et al., 2012) were reported. In the case of kiwifruit, this increase was associated with an elevated soluble solid content, likely a result of altered source-sink relationships induced by the nets (Basile et al., 2012). Furthermore, kiwifruit exposed to 23% shading with R nets showed a decrease in polyphenol concentration and antioxidant activity at fruit harvest, probably due to a decreased UV component in both total and scattered light under the nets (Basile et al., 2012). In contrast, vitamin C content decreased in the fruit of *C. annuum* under 40% shading. However, as vitamin C development is often related to glucose metabolism, R light exposure may affect fruit ripening in a species-specific way (Ilić et al., 2017). Sanchez et al. (2022) reported an increase in leaf area, photosynthetic efficiency, levels of antioxidant enzymes, compounds, osmolytes, and anthocyanin index in *V. planifolia* when grown under 50% R shading condition. In *E. grandiflorum*, total chlorophyll content increased under a 30% R shading environment (Almeida et al., 2021). For *Vaccinium* spp., a 25% R shading level resulted in favourable for increasing fruit size (Zoratti et al., 2015), while a higher

shading percentage (i.e., 80%) delayed the harvest time without detrimental effects on return bloom, yield, or fruit quality in *Vaccinium corymbosum* (Lobos et al., 2013). The application of R-coloured photo-selective nets also resulted in increased yields and phenolic compounds in *Spinacia oleracea* (Lara et al., 2021) and increased yield in *C. annuum* (Ilić et al., 2017), as well as a higher cumulative number of cut cladophylls per plant and per square meter better performance in vegetative parameters in *Asparagus* spp. (Patil et al., 2020), potentially due to a deficiency in BL.

R shading nets, together with B ones, induce a delay in flowering without reducing the production of strawberries (Takeda et al., 2010). B photo-selective films transmit more B and G light while absorbing UV, R, FR, and Y light. This improvement in high-energy wavebands results in increased PSII efficiency and higher photosynthetic performances in different species such as *Allium fistulosum* (Gao et al., 2021), *Ficus carica* (Jokar et al., 2021), *Malus domestica* (Bastías et al., 2012; Mupambi et al., 2018), and *V. planifolia* (Sanchez et al., 2022). It also led to increased levels of photosynthetic pigments in *A. fistulosum*, *C. annuum*, *S. oleracea* and *V. planifolia* (Gao et al., 2021; Ilić et al., 2017; Lara et al., 2021; Sanchez et al., 2022, respectively). Thus, biometric features such as plant height, fresh weight, quality, and yield of green onion, fruit mass in bell pepper, dry weight in spinach, height and leaf area in lemon balm, and total leaf area of apple trees have improved with B photo-selective films (Gao et al., 2021; Ilić et al., 2017; Lara et al., 2021; Oliveira et al., 2016; Bastías et al., 2012, respectively). B nets also influence fruit characteristics, increasing berry size in *Vaccinium* spp. and the apple fruit growth rate (Zoratti et al., 2015; Bastías et al., 2012, respectively), as well as increasing essential oil content in lemon balm (Oliveira et al., 2016). However, there are exceptions reported in the literature regarding the positive vegetative effects of B nets, including, for example, decreased chlorophyll content in basil (Stagnari et al., 2018) and loss of kiwifruit quality, dependent on the reduction in soluble solid content (Basile et al., 2012).

Modifying light quality using G photo-selective coloured shading films, which absorb R and FR lights, decreases the R:FR ratio, phytochrome photo-equilibrium, and solar radiation transmittance, increasing instead the B:FR ratio. In *Beta vulgaris*, G coverings concentrated sugars and minerals in the roots, leading to a decrease in dry weight, TPC, pigment concentration, and antioxidant activity. In basil, this treatment resulted in decreased biomass but increased caffeic acid content in leaves (Stagnari et al., 2014, 2018).

Y photo-selective plastic films, which absorb in the blue-violet region, increased biomass in basil by 28% (compared to G and B films; Stagnari et al., 2018), and improved *B. vulgaris* plant growth (Casierro-Posada et al., 2014a). Moreover, Jokar et al. (2021) reported that fig fruit under Y nets exhibited reduced total soluble solids and titratable acidity but increased antioxidant activity and anthocyanin content. An impairment in photosynthetic performances was recorded in both *F. carica* and *A. fistulosum* (30–36% light shading; Jokar et al., 2021; Gao et al., 2021, respectively). In fig trees, the decreased net photosynthesis and increased photosynthetic pigment content were probably due to the prevalence of G

TABLE 4 Effects of coloured shading nets and films on horticultural species. B – blue net; EO – essential oil; Fv/Fm – maximum quantum yield of PSII; FW – fresh weight; gs – stomatal conductance; G – green net; GR – grey net; NPQ – non-photochemical quenching coefficient; P – pearl net; Pn – net photosynthetic rate; qP – photochemical quenching coefficient; R – red filter; S – silver net; SSC – soluble sugars content; SW – seed weight; V – violet light; W – white net; Y – yellow net; Φ PSII – quantum yield of PSII.

Covering net/film properties	Shade (%)	Species	Effects	Reference
R coloured nets/ films: enhancement of R and FR light transmittance, absorbance of UV, B and G lights	23	<i>Actinidia deliciosa</i>	↑ fruit dry matter, SSC, ↓ polyphenol concentration and antioxidant activity at fruit harvest	Basile et al. (2012)
	50	<i>Asparagus spp.</i>	↑ height, spread, internodal length	Patil et al. (2020)
	40	<i>Capsicum annuum</i>	↑ carotenoids, yield, titratable acidity, ↓ vitamin C	Ilić et al. (2017)
	30	<i>Eustoma grandiflorum</i>	↑ chlorophyll b and total chlorophylls	Almeida et al. (2021)
	30	<i>Fragaria × ananassa</i>	Delaying of the flowering without reducing the number of the runner produced	Takeda et al. (2010)
	40	<i>Malus domestica</i>	↓ photosynthetically active radiation	Bastías et al. (2012)
	65	<i>Spinacia oleracea</i>	↑ yield, phenolic compounds	Lara et al. (2021)
	50	<i>Thymus vulgaris</i>	↑ total chlorophylls, thymol, ↓ growth, carotenoids, EO content and yield, trichome density and diameter, p-cymene	da Cunha Honorato et al. (2023)
	9	<i>Vaccinium spp.</i>	↑ berry size.	Zoratti et al. (2015)
	50	<i>Vanilla planifolia</i>	↑ proportionally red and far-red light, total plant dry weight, leaf area, nocturnal CO ₂ fixation, level of antioxidant enzymes, compounds and osmolytes, anthocyanin index	Sanchez et al. (2022)
B coloured nets/ films: enhancement of B and G light transmittance, absorbance of UV, R, FR and Y lights	27	<i>Actinidia deliciosa</i>	↓ flesh colour, chlorophylls, fruit dry matter %, SSC, polyphenol concentration and antioxidant activity at fruit harvest	Basile et al. (2012)
	30	<i>Allium fistulosum</i>	↑ height, fresh weight, quality, yield, photosynthetic pigment content, Pn, transpiration rate, gs, Fv/Fm, Φ PSII, qP, antioxidant enzymes, absorption and transformation of elements, ↓ active oxygen content	Gao et al. (2021)
	40	<i>Capsicum annuum</i>	↑ chlorophyll a, carotenoids, fruit mass	Ilić et al. (2017)
	33	<i>Ficus carica</i>	↑ stomatal conductance, ↓ dry fruit diameter, total soluble solids	Jokar et al. (2021)
	30	<i>Fragaria × ananassa</i>	Delaying of the flowering without reducing the number of the runner produced	Takeda et al. (2010)
	22	<i>Malus domestica</i>	↑ Fv/Fm, Φ PSII, photochemical reflectance index	Mupambi et al. (2018)
	27		↑ maximal fruit growth rate, fruit weight, leaf photosynthesis, total leaf area	Bastías et al. (2012)
	50	<i>Melissa officinalis</i>	↑ height, leaf area, chlorophyll content, EO yield	Oliveira et al. (2016)
	52	<i>Ocimum basilicum</i>	↑ plant height, leaf pairs on the main stem, number of axillary shoots, leaf area, ↓ leaf thickness, rosmarinic and caftaric acids, chlorophyll content	Stagnari et al. (2018)
	65	<i>Spinacia oleracea</i>	↑ dry weight, antioxidant capacity.	Lara et al. (2021)
	50	<i>Thymus vulgaris</i>	↑ total chlorophylls, thymol, ↓ growth, EO content and yield, trichome diameter, p-cymene, γ -terpinene	da Cunha Honorato et al. (2023)
	15	<i>Vaccinium spp.</i>	↑ berry size, anthocyanin content	Zoratti et al. (2015)
	50	<i>Vanilla planifolia</i>	↑ chlorophyll content, Fv/Fm, level of antioxidant enzymes, compounds and osmolytes, xanthophylls, ↓ nocturnal CO ₂ fixation	Sanchez et al. (2022)
G coloured nets/ films: enhancement of G light	74	<i>Beta vulgaris</i>	↓ dry weight, total phenolic concentration, antioxidant activity, total pigment concentration, ↑ soluble and structural carbohydrates, K, Mg, Zn	Stagnari et al. (2014)

(Continues)

TABLE 4 (Continued)

Covering net/film properties	Shade (%)	Species	Effects	Reference
transmittance, absorbance of R and FR lights	43	<i>Ocimum basilicum</i>	↑ plant height, leaf pairs on the main stem, number of axillary shoots, leaf area, caffeic acid, ↓ biomass, leaf thickness, rosmarinic and caftaric acids	Stagnari et al. (2018)
Y coloured nets/films: enhancement of G, Y and R light transmittance, absorbance of B-V lights	30	<i>Allium fistulosum</i>	↑ intercellular CO ₂ concentration, NPQ, ↓ Fv/Fm, ΦPSII, qP	Gao et al. (2021)
	52	<i>Beta vulgaris</i>	↑ dry weight, leaf area, growth rate, water uptake	Casierra-Posada et al. (2014b)
	27	<i>Capsicum annum</i>	↑ water use efficiency	Casierra-Posada et al. (2014a)
	36	<i>Ficus carica</i>	↑ chlorophylls, carotenoids, relative water content, antioxidant activity, anthocyanins, ↓ net photosynthesis, leaf temperature, ion leakage, titratable acidity, dry fruit diameter, total soluble solids	Jokar et al. (2021)
W coloured nets/films:	20	<i>Actinidia deliciosa</i>	↑ fruit dry matter, ↓ flesh colour, chlorophylls, polyphenol concentration and antioxidant activity at fruit harvest	Basile et al. (2012)
	30	<i>Allium fistulosum</i>	↑ height, fresh weight	Gao et al. (2021)
GR coloured nets/films	27	<i>Actinidia deliciosa</i>	↓ fruit dry matter %, SSC, polyphenol concentration and antioxidant activity at fruit harvest	Basile et al. (2012)
	50	<i>Asparagus</i> spp.	↑ leaf production, leaf area, number of cut cladophylls per plant and per square meter, vase life	Patil et al. (2020)
	40	<i>Malus domestica</i>	↑ maximal fruit growth rate.	Bastías et al. (2012)
B-GR coloured nets/films	20	<i>Corylus avellana</i>	↓ vapour pressure deficit, stomata density, specific leaf weight	Salazar-Canales et al. (2021)
P-GR coloured nets/films	20	<i>Corylus avellana</i>	↑ yield, FW, and SW, ↓ vapour pressure deficit.	Salazar-Canales et al. (2021)
P coloured nets/films	40	<i>Capsicum annum</i>	↑ yield, titratable acidity, ↓ palisade parenchym	Ilić et al. (2017)
S coloured nets/films	40	<i>Lactuca sativa</i>	↓ stomatal density, chlorophyll content, carotenoids	Rossi Pinheiro et al. (2020)

wavelengths under this treatment, which strongly influenced stomatal conductance (Folta & Carvalho, 2015).

Other coloured photo-selective nets that can be used are white, grey, or silver. White nets effectively increased plant height and fresh weight in green onion (Gao et al., 2021), while in kiwi-fruit, despite the higher dry matter, white shade nets induced slight negative effects on flesh colour and chlorophyll concentration (Basile et al., 2012). Grey nets negatively affected fruit dry matter and soluble solids content in *A. deliciosa* fruit due to the higher shading percentage in these nets compared to others (Basile et al., 2012). Pearl-gray nets significantly increased accumulated yield, fruit weight, and seed weight (12, 13, and 6%, respectively, compared to the control - i.e. uncovered trees) in *Corylus avellana*. In the same experiment, B-grey shade nets resulted in a decline in net photosynthesis, which was attributed to non-stomatal limitations and changes in leaf morphology (Salazar-Canales et al., 2021). Grey nets also had a positive effect

on apple fruit growth rate, *Asparagus* spp. leaf production and number in cladophylls, as well as pepper fruit yield (Bastías et al., 2012; Patil et al., 2020; Ilić et al., 2017, respectively). Finally, silver coverings, reflecting a large amount of incident solar radiation, may strongly alter the microclimate under the net, thereby leading to changes in leaf transpiration as well as photosynthetic pigments, as observed in lettuce (Rossi Pinheiro et al., 2020). However, the concentration of chlorophylls and carotenoids showed variations dependent upon the cultivar, demonstrating the genotype-dependent responses to these silver nets.

4.3 | Fluorescent photo-converting films

Technology in polymer materials used in agricultural films has continuously improved. Currently, the trend is to employ light conversion agents in the polymer film manufacturing process to introduce

wavelength conversion capabilities to greenhouse materials. These agents include fluorescent dyes, organic rare-earth complexes, and inorganic rare-earth complexes, which are designed to convert sunlight into specific wavelength ranges suitable for plant growth and, more specifically, plant photochemical processes (Figure 1; Table 5) (Liu et al., 2022). Notwithstanding, a critical factor in selecting this technology is the photophysical properties, particularly the photostability of the material under extreme weather conditions, including intense irradiation. Such conditions can cause a strong decrease in the light absorption and, consequently, loss of photo-conversion properties (Ooyama et al., 2012).

Thanks to their photophysical and chemical properties, the incorporation of nanosized inorganic particles into polymer matrices absorbs the green-yellow range of visible solar spectra and fluoresce or re-emit it as either RL (El-Bashir et al., 2016) or conversion of UV to BL (Kang et al., 2018). At present, nanoparticles with plasmon or exciton emission are used; the most popular pairs are cadmium-selenium (Fitzmorris et al., 2013) or gold-sulfur (Pu et al., 2018). However, there are significant difficulties with the inclusion of these pigments in polymer matrices, as well as a problem with their susceptibility to reactive oxygen species, which are always formed in vapour-permeable materials. Other agents, such as the rare-earth materials for light conversion films, increased transmittance and photosynthetic range of B, R-orange, and FR light, whereas UV, purple, and GL decreased inside the greenhouse.

Examining the effect of a rare-earth-complex light conversion film on leaf structure, Gao et al. (2022) observed that sweet pepper leaves from plants grown under these films exhibited increased thickness and longer stomata than those grown with a polyolefin film (used as control). Furthermore, endogenous hormone content in sweet pepper fruit, specifically gibberellic acid 3 (GA3) and/or indole-3-acetic acid (IAA), was significantly higher in plants grown under the rare-earth material light conversion film. These results underscore the ability of R light to activate PHYA and PHYB coupled with GA3 biosynthesis (Gao et al., 2022). Hemming et al. (2006) investigated the optimal concentration of blue fluorescent pigments for converting UV radiation into BL and evaluated the increment level of light intensity inside the greenhouse. Fluorescence effects of the plastic film prototypes were rising with increasing pigment concentration, and though fluorescent effects by blue pigments increased total PAR transmission by only 1–3%, the fluorescent film with high blue pigment concentration resulted in an increase in strawberry fruit number, thereby suggesting this film has good potentials to improve strawberry production (Hemming et al., 2006).

The challenge of designing a durable and resistant spectrum conversion film urged Nishimura et al. (2012) to investigate its effects on cucumber plants development and nutrient absorption. Natural light-type film was compared with a spectrum conversion film that converted part of the G wavelength range to R wavelengths (Nishimura et al., 2012). The results showed that cucumber fruit and leaves from plants grown with the spectrum conversion film were richer in P in comparison with those grown under a neutral light film (control), with no significant differences in macronutrients such as K, Mg and Ca (Nishimura et al., 2012). Phosphorous plays a crucial role in plant

physiology, serving as an essential element for ATP energy production and contributing significantly to carbon metabolism during both photosynthesis and respiration. Phosphorous deficiency is known to inhibit photosynthetic rates by depressing the Calvin cycle activity and reducing stomatal conductance, ultimately limiting nitrate uptake and, thus, chlorophyll biosynthesis (Naureen et al., 2018). The higher level of P may have allowed the activation of photosynthesis in both cucumber fruit and leaves under the spectrum conversion films, resulting in faster plant growth. This was evident in the substantial increase in total leaf fresh weight (+49% under the conversion film compared to natural light film) and total fresh weight (+41% under the conversion film compared to natural light film) observed in both cases (Nishimura et al., 2012).

In another study, R-shifting films increased yield, photosynthetic rates, total soluble sugars, and vitamin C content in lettuce, proving to be even more convenient under low-light environmental conditions (Shen et al., 2021; Li et al., 2022). González et al. (2003) observed an increased vegetative growth in cucumber plants under fluorescent covers. However, this did not correlate with fruit production, as a decrease was observed in fruit yield using an orange fluorescent film and a decrease in fruit weight under a magenta fluorescent film.

In regions with distinct climatic conditions, photoconversion films have proven to be suitable for areas frequently characterized by low temperatures and low photosynthetic light, such as high latitudes. Apart from the UV conversion into B and R wavelengths, the photoconverting films tested by Gudkov et al. (2020) demonstrated the capacity to convert the G sunlight waveband into heat and R light acknowledged to be in line with high latitudes cultivated crops needs. From the physiological point of view, tomato plants grown in greenhouses covered with polymer film packed with fluorophores for photoconversion technology exhibited a remarkable increase in chlorophyll content (+55%) and a significant improvement in CO₂ assimilation (30–40%) compared to plants under standard polymer film (Gudkov et al., 2020).

In conclusion, the reaction of certain crops to light alterations, ΦPSII such as UV radiation exclusion, the enhancement of the light distribution or the selection of certain wavelengths from the spectrum of light absorbed by the plant inside the structure may yield neutral or dynamic reactions. Thereafter, the choice between employing plastic films with single or multiple functionalities to address plant metabolite concentrations should be guided by economic feasibility and, most importantly, by the results desired by farmers (Papaioannou et al., 2012; Zheng et al., 2020; Gudkov et al., 2020).

4.4 | Light-diffusing plastic film for canopy species

For crops with significant canopy volumes, the solar radiation distribution inside the greenhouse/tunnel is not always at its optimum due to the canopy shading with limited incident light reaching bottom leaves compared to the upper part of the canopy. This issue can be solved by using light-diffusing plastic films designed to distribute solar radiation,

TABLE 5 Classification of fluorescent photo-converting covering films according to the description in the referring scientific paper. B – blue light, FR – far-red light; G – green light; O – orange light; R – red light; UV – ultra-violet light; V – violet light; Y – yellow light.

Light shift	Species	Effects	Reference
Fluorescent orange; Fluorescent magenta: UV absorption and conversion of B and G radiation into R light. Alteration of R:FR relation	<i>Cucumis sativus</i>	↑ vegetative growth; orange film, ↓ yield; magenta film, ↓ fruit weight	González et al. (2003)
	<i>Fragaria × ananassa</i>	↑ yield	
Fluorescent blue: UV radiation conversion into B light	<i>Fragaria × ananassa</i>	↑ yield, fruit number, fruit size	Hemming et al. (2006)
Ethylene tetrafluoroethylene spectrum conversion film: G radiation conversion into R light	<i>Cucumis sativus</i>	↑ fruit yield, growth, fruit dry matter, P concentration in leaf and fruit, other mineral element concentration	Nishimura et al. (2012)
Gold nanoparticles fluoropolymer: UV and V radiation conversion into B and R light. G radiation partial conversion into heat	<i>Capsicum annuum</i> ; <i>Cucumis sativus</i> ; <i>Solanum lycopersicum</i> ; <i>Solanum melongena</i>	↑ growth rate, assimilation rate, chlorophyll content	Gudkov et al. (2020)
Fluorescent red: G radiation conversion into R light	<i>Lactuca sativa</i>	↑ production, plant diameter, leaf area, leaf number, leaf length	Shen et al. (2021)
Light conversion film: Y-G radiation conversion into R-O light	<i>Lactuca sativa</i>	↑ photosynthetic rate, yield, total soluble sugars, reduction-type Vitamin C	Li et al. (2022b)
Rare-earth light conversion film: UV, V, and G radiation conversion into B, R-O, and FR light	<i>Capsicum annuum</i>	↑ plant height, stem diameter, internode length, Gibberellic acid 3, Indole-3-acetic acid, Zeatine Riboside, fruit yield, ascorbic acid, soluble protein, soluble sugars, net photosynthesis, Rubisco activity and Rubisco small subunit transcription	Gao et al. (2022)

reducing the shade effect within the canopy (Zheng et al., 2020; Ávalos-Sánchez et al., 2022). These films increase solar energy availability and distribute direct light to different leaf levels (Holcman et al., 2015). Plastic film with 29% haze, resulting in more uniform PPFD directions to lower and middle canopies and higher leaf photosynthesis (Zheng et al., 2020; Moreno-Teruel et al. 2021). The functions of diffusing plastic films and their agronomic use are described in Table 6.

Plants take advantage of diffuse light, leading to improved productivity. For example, in cucumber cultivation, an experimental film with 55% light diffusion improved marketable yield by 5% in the first growth cycle and 15% in the second cycle (Ávalos-Sánchez et al., 2022). Diffusive plastic films have been shown to allow greater incidence of solar radiation inside glasshouses without causing major changes in air temperature and relative humidity, ensuring higher productivity (Holcman et al., 2015).

The unique structure of these films increased the fraction of diffuse light, improving the uniformity of the light environment and guaranteeing higher performance not only in terms of photosynthesis but also in terms of leaf metabolite composition. For example, an increase in tocopherol, carotenoid and chlorophyll content was found in tomato grown with a diffusive film compared to a conventional polyethylene-based one (Petropoulos et al., 2019). However, light-diffusive films have also been reported to increase nitrate content in *L. sativa* and *Valerianella locusta* (Riga & Benedicto, 2017; Cozzolino et al., 2020), which need to be considered in view of the Commission Regulation (EC) No 1881/2006 which fixes maximum nitrate levels in some leafy vegetables, including lettuce.

4.5 | Coloured mulching films

In the case of deploying coloured films exclusively on the below-ground area, R plastic film has shown positive results in the form of mulch. R plastic film is able to reflect more FR and R lights and has a lower R:FR ratio compared to black plastic mulch. However, in some cases, the use of B plastic film alternated with R films (Zhou et al., 2023) may exert positive results. The functions of coloured films used as mulching are described in Table 7.

Under R plastic mulch, Shiukhy et al. (2015) reported a phytochrome-mediated gene expression leading to enhanced aroma compounds and increased fruit production (34%) in strawberry plants cv. Camarosa. Although no significant differences were observed between treatments for the content of fruit phenolic compounds, the concentration of anthocyanins and flavonoids was higher in fruit from plants grown over an R plastic mulch (Shiukhy et al., 2015). Another experiment by Zhou et al. (2023) demonstrated that in grape the use of R, B, R and B mulching films strongly influenced the photosynthetic rate, leaf photosynthetic pigments, as well as the activities of both sucrose synthase and invertase in leaves. In particular, the alternation of R with B mulching films exerted the best effects, which resulted in higher total soluble solids in fruits. All these studies suggest that coloured mulching films are a valuable tool to modulate light quality below the plant canopy, thereby improving fruit carbohydrate contents by regulating leaf photosynthetic pigments and sucrose metabolism enzyme activities.

Of note, the effect of mulch colour on plant growth and yield may vary according to the geographic location and season (Csizinszky

TABLE 6 Classification of light-diffusing plastic films according to the description in the referring scientific paper.

Film characteristics	Species	Effects	Reference
55% of diffusive capacity	<i>Solanum lycopersicum</i>	↑ productivity	Holcman et al. (2015)
Two polyethylene films, one simple and one double, with low diffusion fraction and an external 50% transmission to infrared radiation and an internal 18% transmission to infrared radiation; 90% transmission to solar radiation		↑ tocopherol, carotenoids, and chlorophyll contents. ↓ sugar content	Petropoulos et al. (2019)
Two ethylene-vinyl acetate films with 20 and 29% haze respectively 89% transmission		↑ yield and photosynthetic activity	Zheng et al. (2020)
Transmission of photosynthetically active radiation of 0.90 55% light diffusion 90% thermal efficiency		↑ marketable yield and photosynthetic activity	Moreno-Teruel et al. (2021)
>90% light diffusion ≥88% light transmission	<i>Lactuca sativa</i>	↑ microelement, nitrate and soluble solid contents, acidity. ↓ biomass, leaf number, leaf area, photosynthetic activity, pigment content and leaf pH	Riga and Benedicto (2017)
light diffusing polyethylene-based film	<i>Valerianella locusta</i>	↑ SPAD index, yield, ascorbic acid, and nitrate content	Cozzolino et al. (2020)

TABLE 7 Classification of functional mulching films according to the description in the referring scientific paper. Chl – chlorophylls; FR – far-red light; FW – fresh weight; GR – grey; P_n – net photosynthesis; R – red light; RS – reducing sugars; S – silver; S:A – sugars: acid; TA – titratable acidity; TSS – total soluble solids; Y – yellow; W – white.

Covering film classification	Film characteristics	Species	Effects	Reference
Coloured film	R film: ↓ R:FR ratio of reflected light	<i>Fragaria × ananassa</i>	↑ fruit weight, size, yield, anthocyanin content	Shiukhy et al. (2015)
	W, S and GR film: W ↓ root-zone temperature. S ↑ light reflectance	<i>Solanum lycopersicum</i>	Spring season: GR and S ↑ vegetative FW. W ↓ fruit FW, fruit number per plant, fruit yield. Fall season: GR and S ↑ vegetative and fruit FW, fruit number per plant, fruit yield	Díaz-Pérez and Batal (2002)
	R, B and R ± B: increase the proportion of R, B and R + B light respectively below plant canopy	<i>Vitis vinifera</i>	R ↑ chl, RS, S:A ratio; ↓ acid and neutral invertase. B ↑ acid and neutral invertase; ↓ TSS, sucrose, S:A ratio. R + B ↑ P _n , chl, sucrose and sucrose phosphate synthase, TSS, RS, S:A ratio; ↓ TA.	Zhou et al. (2023)
Photo-selective film	Y polyethylene film: ↓ soil temperature	<i>Capsicum annuum</i> ; <i>Cucumis melo</i>	↑ root mycorrhizal (%)	Bonanomi et al. (2017)
		<i>Lycopersicon esculentum</i> ; <i>Citrullus lanatus</i> ; <i>Brassica oleracea</i> var. <i>gongylodes</i>	↑ yields	

et al., 1995), suggesting that plants grown on coloured mulches respond to other factors in addition to the light reflected from the mulch, such as the mulch-related cooling factor. Indeed, besides the use of photo-selective films for the positive effect on photosynthesis and fruit phytochemical quality, their application on the root zone areas is worth investigation due to their ability to maintain cooler soil temperatures compared to black mulch (the most used) that occasionally impairs plant growth due to high root-zone temperatures (Díaz-Pérez & Batal, 2002). For example, tomato plants exposed to a range

of root-zone temperatures, resulting from growing the plants in different seasons and by using coloured mulches that differed in reflectance, showed a + 15% increase in tomato fruit yield (coloured versus black mulch) due to a low root-zone temperature provided by the coloured film (−0.5°C) (Díaz-Pérez & Batal, 2002). Similarly, photo-selective mulching films applied at the root zone showed an increase in crop irrigation water productivity compared with black film by 25% in sweet pepper, tomato, lettuce, melon, and kohlrabi with the most positive results observed in winter crops (Bonanomi et al., 2017).

Indeed, though mulching films showed similar water-saving prerogatives to those of a black film, soil temperature and plant evapotranspiration under photo-selective mulching films were consistently lower than that under B mulch.

5 | LIGHT DISTURBANCE: THE CASE OF STREETLAMP ILLUMINATION ON TREES

Although there are benefits to supplemental lighting in greenhouse cultivation, artificial illumination may negatively affect plant physiology. This is particularly evident in urban areas, where streetlamps extend the “day length” throughout the night. In our cities, light pollution has constantly risen by around 6% per year over the last decades to facilitate human activities (Hölker et al., 2010), altering animal behaviour, like herbivores and pollinators, and affecting plant phenology, growth, and resource allocation (Lian et al., 2021; Liu et al., 2021; Lo Piccolo et al., 2023). The first observations of this phenomenon on plants occurred in the first half of the 20th century when Matzke (1936) observed a delay in leaf senescence in trees growing in close proximity to streetlamps (e.g., in *Populus canadensis* and *Platanus × acerifolia* individuals). Subsequently, Chaney (2002), compiled a comprehensive table detailing the susceptibility of woody plants to the influence of illumination from streetlamps. However, since then, only a handful of studies have investigated the repercussions of light pollution on trees, and even fewer have explored the physio-chemical traits of plants illuminated by streetlamps at night. Furthermore, no one has ever studied the long-term effect of night illumination on tree health and ecosystem services. Consequently, much of the real amplitude of this phenomenon remains to be thoroughly understood and elucidated.

In plants, photoreceptors (i.e., phytochromes, cryptochromes, and phototropins) are pivotal for regulating circadian rhythms based on external light stimuli, perceiving seasonal changes, controlling the repair and recovery of plant physiological functions, and inducing the onset of flowering and dormancy (Björn, 2015; Kong & Zheng, 2020). In this framework, it seems obvious that night streetlamp illumination could influence plant circadian rhythms by interfering/stimulating photoreceptors (Bennie et al., 2016; Bennie et al., 2017). The light emission spectrum of streetlamp illumination can vary greatly depending on the technology (Bennie et al., 2016). In the urban environment, the most common streetlamp solutions used in the past were High-Pressure Sodium (HPS) lamps, with high irradiance peaks in the R spectrum, which are highly likely to interfere with plant phytochromes. However, more recently, HPS lamps have been gradually replaced by LED lamps, causing different problems for tree metabolism, as these lamps have an additional peak in the B light emission spectrum (Lo Piccolo et al., 2023), which interferes with plant cryptochromes. These photoreceptors regulate stem growth, flowering time, stomatal opening, circadian clock, and other UV/BL-driven responses (Wang & Lin, 2020). Among others, one of the main reactions triggered by cryptochrome is the BL-induced stomatal response, which occurs at low light intensities and is often considered

independent of photosynthesis (Violet-Chabrand et al., 2021). However, some studies demonstrated that the intensity of RL over BL influences the magnitude of the stomatal response (Shimazaki et al., 2007), considering that this ratio varies during the day and plants experience a high BL:RL at dawn and before dusk (Matthews et al., 2020). Therefore RL:BL, as well as the addition of GL on the streetlamp spectra (which is opposite the effect of BL on cryptochromes; Johkan et al., 2012; Landi et al., 2020) should be considered to develop less impacting streetlamps on tree species.

To date, information on the effects of specific streetlamp technologies on plant physiology is scarce, largely due to the lack of investigation into different streetlamp technologies and the species-specific nature of these effects. Therefore, the following text will discuss the general impacts of nocturnal illumination by streetlamps on trees. Table 8 outlines the multiple effects on plant phenology and physiology due to streetlamp illumination on trees.

In general, nocturnal illumination by streetlamps leads to a delay in the autumn leaf fall and the entry into winter dormancy, as was observed in *P. canadensis* and *P. occidentalis* (Matzke 1936), *P. × acerifolia* (Massetti, 2018; Lo Piccolo et al., 2023), *Rhus typhina* (Tuhárska et al., 2014; Škvareninová et al., 2017) and *Acer pseudoplatanus* (Škvareninová et al., 2017) (Figure 4). These delays could potentially have adverse consequences for deciduous trees, especially in the presence of frosts, which may damage leaves and buds.

On the contrary, no alterations in the tree phenology were observed in *Betula pendula* and *Tilia × platyphyllos* (Sarala et al., 2013, Lo Piccolo et al., 2023, respectively). These differential responses among tree species could be due to the species-specific sensitivity to external stimuli, as winter dormancy can be influenced by factors such as photoperiod and temperature, or the combination of both (Zhang et al., 2020). Lo Piccolo et al. (2023) observed that the entry into winter dormancy of *T. × platyphyllos* was less influenced by the altered photoperiod, suggesting that external environmental temperatures played a more significant role in regulating dormancy induction than the photoperiod. On the other hand, in the case of *B. pendula*, both photoperiod and temperature can influence the onset of winter dormancy (Junttila et al., 2003, Li et al., 2003b). Therefore, the absence of an influence in tree phenology observed by Sarala et al. (2013) could be due to the low light intensity tested ($0.16 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the sampling point).

A 13-year-long investigation conducted in the UK on spatially referenced budburst data from four deciduous tree species, matched with satellite imagery of night-time, unveils that streetlamp night illumination anticipate bud burst by 7.5 days on brighter areas affecting particularly later-budding species (Ffrench-Constant et al., 2016). Similarly, an experiment with four tree and four shrub species found that all the species investigated were influenced by artificial light at night and developed buds faster than the control group (Czaja & Kolton, 2022). Moreover, it was reported that night light pollution could lead to an anticipated start of the growing season in the climatically temperate regions of the USA, though in colder or hotter regions, environmental temperatures have a predominant role in the induction of the spring phenology (Zheng et al., 2021). On the contrary, Lian

TABLE 8 Effects of streetlamp illumination on trees and shrubs. Works are gathered in chronological order. HPM – high-pressure mercury lamps; HPS – high pressure sodium; FLS – Fluorescent lamps; LED – light emitting diode; PAR – photosynthetically active radiation; ABA – abscisic acid; PI_{ABS} – performance index for energy conservation from photons absorbed by PSII antenna, to the reduction of Q_B ; F_v/F_m – maximum quantum yield of PSII; Φ_{PSII} – quantum yield of PSII; $\Phi(NPQ)$ – Quantum yield of light-induced nonphotochemical fluorescence quenching; $\Phi(NO)$ – quantum yield of non-light-induced non-photochemical fluorescence quenching; P_n – net CO_2 assimilation.

Plant species	Lamps	Treatment	Effects	Reference
<i>Betula pendula</i>	HPM lamps	PAR 0.16 $\mu\text{mol m}^{-2} \text{s}^{-1}$, at sampling point, ranging from 6 to 10.5 h	No effects on chlorophyll and carotenoid contents	Sarala et al. (2013)
<i>Rhus typhina</i>	FLS lamps	-	Delay of the autumn phenological phase of leaf colouring in some crown parts of several trees	Tuhárska et al. (2014)
<i>Acer pseudoplatanus</i> <i>Fagus sylvatica</i> <i>Quercus robur</i> <i>Fraxinus excelsior</i>	-	-	Advance in budburst (up to 7.5 d) in deciduous trees, especially in later-budding species	Ffrench-Constant et al. (2016)
<i>Liriodendron tulipifera</i>	HPS lamps	PAR 0, 1, 3, 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$, for 11 h	↓ stomatal aperture and stomatal size ↓ stacked grana thylakoid membranes Dawn: ↑ ABA content, ↓ degradation of ABA Dusk: ↓ starch and ABA contents Night: ↓ starch degradation	Kwak et al.
<i>Acer pseudoplatanus</i> <i>Rhus typhina</i>	HPS and LED lamps	Light pollution of 2.9, 6.5 or 9.6 lx depending on the area and lamp technology. Measures were taken at 1.3 m under the light source	Delay of 13 to 22 days on the onset of the autumn phenophase. Duration of leaf fall was prolonged by 6 to 7 d	Škvareninová et al. (2017)
<i>Liriodendron tulipifera</i>	HPS lamps	PAR 0, 1, 3, 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$, for 11 h	↓ plant biomass, ↓ chlorophyll contents ↓ PI_{ABS} ↑ H_2O_2 and O_2^- contents Premature leaf senescence and leaf tissue necrosis	Kwak et al. (2018)
<i>Platanus × acerifolia</i>	HPS lamps	Between 7.9 and 12.8 $W m^{-2}$	Delay on the onset of the autumn phenophase	Massetti (2018)
<i>Calotropis procera</i> <i>Butea monosperma</i> <i>Delbergia sissoo</i> <i>Azadirachta indica</i> <i>Plumeria rubra</i> <i>Eucalyptus globulus</i> <i>Bauhinia purpurea</i>	-	340–360 lx at sampling point	↓ F_v/F_m , Φ_{PSII} and $\Phi(NPQ)$ ↑ $\Phi(NO)$	Meravi and Prajapati (2018)
<i>Cinnamomum camphora</i>	-	-	↑ leaf chlorophyll content ↑ diameter at breast height ↑ branch growth	Li et al. (2019)
<i>Aesculus hippocastanum</i> <i>Alnus glutinosa</i> <i>Betula pendula</i> <i>Fagus sylvatica</i> <i>Fraxinus excelsior</i> <i>Quercus robur</i> <i>Tilia cordata</i>	-	Dataset of measures from 1992 to 2015	Plant phenological phases are substantially delayed	Lian et al. (2021)
<i>Acer truncatum</i> <i>Quercus mongolica</i>	LED lamps	PAR 80 $\mu\text{mol m}^{-2} \text{s}^{-1}$, for 5 h	↑ shoot biomass ↑ carbohydrate production N dilution	Liu et al. (2021)
<i>Tilia × platyphyllos</i> <i>Platanus × acerifolia</i>	LED lamps	PAR 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at sampling point	Nocturnal CO_2 assimilation ↑ leaf chlorophyll content Circadian rhythmicity of chlorophylls was not affected	Lo Piccolo et al. (2021)

(Continues)

TABLE 8 (Continued)

Plant species	Lamps	Treatment	Effects	Reference
<i>Tilia tomentosa</i> <i>Betula pendula</i> <i>Fagus sylvatica</i> 'Purpurea' <i>Acer campestre</i> <i>Cornus alba</i> <i>Lonicera pileata</i> <i>Kerria japonica</i> 'Pleniflora' <i>Spiraea</i> × <i>cinerea</i> 'Grefsheim'	LED lamps	Experiment conducted in light chambers. PAR 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during the day and PAR 0, 1 or 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during the night	<p>↑ bud developing (up to 20 days, depending on the species, with the highest acceleration observed in <i>K. japonica</i>)</p> <p>↑ soluble sugars content in branches of <i>L. pileata</i> and <i>C. alba</i></p> <p>↓ soluble sugars content measured in apical twigs of <i>T. tomentosa</i>, <i>S. × cinerea</i>, <i>K. japonica</i> and <i>A. campestre</i></p>	Czaja and Kołton (2022)
<i>Tilia</i> × <i>platyphyllos</i> <i>Platanus</i> × <i>acerifolia</i>	LED lamps	PAR 700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and of 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ measured at the canopy level	<p>↓ Pn at sunrise</p> <p>↑ chlorophyll contents at leaf mature stage</p> <p>↓ starch accumulation</p> <p>↑ starch degradation rate in young and mature leaves of <i>T. × platyphyllos</i>, and in mature and senescent leaves of <i>P. × acerifolia</i></p> <p>Delay of winter dormancy by two months in <i>P. × acerifolia</i></p>	Lo Piccolo et al. (2023)



FIGURE 4 Influence of the streetlamp lighting on *Platanus* × *acerifolia* trees. The image is relative to the delay of the leaf senescence phenomenon during wintertime (December 2022, Florence, Italy).

et al. (2021), observed a delay in leaf burst in *Alnus glutinosa*, *B. pendula* and *F. excelsior* grown in light-polluted areas in Europe between 1991–2015. The apparent contradictions in these findings may be due to the fact that little research has been performed on the

interactive effects of urban environmental temperatures (e.g., heat islands) and streetlamp illumination (e.g., if it heats, its light spectrum, its brightness) on urban tree phenology. Lian et al. (2021) suggested that while temperature plays a dominant role in shifts in plant phenological phases, the delaying effect of artificial light pollution is evident when considering these interactions.

In the literature, there are conflicting reports regarding the effect of streetlamp illumination on leaf pigments of urban trees, which, again, suggests the species-specificity of this response. Kwak et al. (2018) reported that leaves of plants exposed to streetlamp illumination rapidly turned yellow and fell. In contrast, Sarala et al. (2023) found no significant differences in leaf chlorophyll content in *B. pendula* trees exposed to streetlamps, whilst Li et al. (2019) reported higher values in leaf chlorophyll content in *Cinnamomum camphora*. Interactions between external light signals and the endogenous plant circadian clock regulate chlorophyll biosynthesis and breakdown. For instance, the conversion from protochlorophyllide to chlorophyllide is light-dependent, thus, this control mechanism leads to decreased chlorophyll synthesis at night and increased synthesis during the day (Kobayashi & Masuda, 2019; Kumar et al., 2020; Suzuki & Bauer, 1995). Lo Piccolo et al. (2023) argued that nighttime lighting provided by streetlamps hampered the natural decrease in chlorophyll biosynthesis during the night, thus explaining the higher chlorophyll content in the leaves of trees grown under streetlamp illumination and possibly increasing the demand for N assimilation by the leaves. This assumption agrees with the observations of Liu et al. (2021), who reported low N concentrations in the roots and wood of trees illuminated by streetlamps, probably due to an increased demand for N assimilation by leaves and, subsequently, more chlorophyll biosynthesis. The contrasting results reported by Kwak et al. (2018) were probably linked to a premature leaf senescence phenomenon stemming from oxidative damage produced by high levels of ROS, such as O_2^- and H_2O_2 , which led to increased lipid peroxidation and membrane permeability under artificial night illumination.

Nighttime illumination, if of sufficient intensity, can induce plants to photosynthesise during nocturnal hours (Lo Piccolo et al., 2021, 2023; Kwak et al., 2018), although the observed values of net photosynthesis (P_n) were lower than those at sunrise. Kwak et al. (2017) suggested that artificial nighttime light may unbalance the endogenous circadian levels of ABA, resulting in stomatal opening. The reduced P_n values at dawn may also be related to impairment of the photosynthetic machinery. Indeed, as observed in *Populus alba*, the greatest reductions in PSII performances were observed at dawn, where the lack of starch degradation during the night and the relative impairment in the sinking capacity, which may induce a feedback limitation, thus impairing linear electron transport flow, also evidenced by the downregulation of two ferredoxin nitrite/sulphite reductase domains (Lo Piccolo et al., 2024). Furthermore, the abundance of light-harvesting complex (LCHII) of PSII also exhibited a reduction in *L. tulipifera* (Kwak et al., 2017). Nocturnal alterations in photosynthesis due to streetlamp lighting can alter the primary metabolism of illuminated leaves, consequently impairing the source/sink balance. Kwak et al. (2017) observed a carbon starvation phenomenon in the leaves of *L. tulipifera*, resulting from reduced daytime accumulation and decreased nighttime starch degradation. Liu et al. (2021) observed an increase in starch and total soluble sugar concentrations in *Acer truncatum* and *Quercus mongolica* in streetlamp-lighted trees due to an accelerated translocation of carbon to sinks (i.e., new shoots that remained active even during the winter; Lo Piccolo et al., 2023).

The few observations obtained from the literature regarding leaf primary metabolism and carbon content suggest that tree species may adopt different strategies in response to nighttime streetlamp illumination, emphasising differences in susceptibility to artificial night lighting and highlighting the fact that this topic still needs to be fully elucidated.

All of the aforementioned reports highlight the deep influence of streetlamp lighting on urban trees. However, it is important to note that streetlamps do not only affect trees but also grass species, inducing vegetation changes in biomass and plant cover over time (i.e., *Agrostis tenuis*, *Anthoxanthum odoratum* and *Holcus lanatus*; Bennie et al., 2017).

To strike a balance between citizen safety and the well-being of urban vegetation, more research is required to fully understand both the annual and long-term impacts that urban illumination has on ecosystem functioning. It is necessary to investigate the effects of different streetlamp technologies, test innovative light spectra enriched with green and orange wavelengths and provide a comprehensive list of tree species susceptibility to artificial nocturnal lighting. Such research could help urban planners select the proper tree species for roadside avenues and lessen the impact of lighting solutions in our cities without compromising the fundamental need for citizen safety.

6 | CONCLUSION AND PERSPECTIVES

The capabilities of new light technologies and cutting-edge materials for covering films to improve plant growth as well as metabolic

performance have been increasingly exploited. The trade-off between costs and benefits (which goes beyond the aim of the present review) has to be considered and contextualized for each species. However, it is undeniable that “photomodulation” is a powerful tool to shape plant morpho-anatomical and metabolic features, though a lot of aspects still need to be investigated. For example, improving light use efficiency by the plant, even in condition of fluctuating light, is a frontier topic of investigation to feed a constantly growing population. On the other hand, artificial lighting may exert negative side effects, i.e. light pollution in urban environments, posing the urgent need for less-impacting streetlamp spectra on tree physiology. Besides the methodologies for light management proposed herein, some others for which the research and application are in their infancy are still worth mentioning. For example, root illumination in hydroponic cultivation (Cabrera et al., 2022) and fruit bagging (i.e. the use of coloured plastic films; Ali et al., 2021) could be proficiently used as an unconventional method to promote the quality and development of horticultural species. To date, few reports are available on these topics, and few details are provided regarding the spectra supplied to plants, which makes the result unreliable for drawing any solid and consistent conclusions. Thus, scientists and growers have nowadays a unique opportunity to contribute to generating knowledge on existing products for light management, while companies have the possibility to extend the portfolio of available products through cutting-edge innovation on light technologies and photomodulating materials.

ORCID

Ermes Lo Piccolo  <https://orcid.org/0000-0001-9789-2524>

Marco Landi  <https://orcid.org/0000-0003-0121-0715>

REFERENCES

- Abdoul, D., Soufi, S., Bettaieb, T. & Werbrouck, S.P. (2023) Effects of monochromatic light on growth and quality of *Pistacia vera* L. *Plants*, 12(7), 1546. <https://doi.org/10.3390/plants12071546>
- Abou El-Dis, G.R., Zavdetovna, K.L., Nikolaevich, A.A., Abdelazeez, W.M.A. & Arnoldovna, T.O. (2021) Influence of light on the accumulation of anthocyanins in callus culture of *Vaccinium corymbosum* L. cv. Sunt Blue Giant. *Journal of Photochemistry and Photobiology*, 8, 100058. <https://doi.org/10.1016/j.jpap.2021.100058>
- Adil, M., Abbasi, B.H. & ul Haq, I. (2019) Red light controlled callus morphogenetic patterns and secondary metabolites production in *Withania somnifera* L. *Biotechnology Reports*, 24, e00380. <https://doi.org/10.1016/j.btre.2019.e00380>
- Affandi, F.Y., Verdonk, J.C., Ouzounis, T., Ji, Y., Woltering, E.J. & Schouten, R.E. (2020) Far-red light during cultivation induces postharvest cold tolerance in tomato fruit. *Postharvest Biology and Technology*, 159, 111019. <https://doi.org/10.1016/j.postharvbio.2019.111019>
- Ahmad, N., Rab, A. & Ahmad, N. (2016) Light-induced biochemical variations in secondary metabolite production and antioxidant activity in callus cultures of *Stevia rebaudiana* (Bert). *Journal of Photochemistry and Photobiology B: Biology*, 154, 51–56. <https://doi.org/10.1016/j.jphotobiol.2015.11.015>
- Ali, M.M., Anwar, R., Yousef, A.F., Li, B., Luvisi, A., De Bellis, L., Aprile, A. & Chen, F. (2021) Influence of bagging on the development and quality of fruits. *Plants*, 10(2), 358. <https://doi.org/10.3390/plants10020358>
- Almeida, J.M.D., Calaboni, C. & Rodrigues, P.H.V. (2021) Pigments in flower stems of lisanthus under different photosensitive shade nets.

- Ornamental Horticulture*, 27, 535–543. <https://doi.org/10.1590/2447-536X.v27i4.2389>
- Amaki, W., Yamazaki, N., Ichimura, M. & Watanabe, H. (2011) Effects of light quality on the growth and essential oil content in sweet basil, *Acta Horticulturae*, 91–94. <https://doi.org/10.17660/ActaHortic.2011.907.9>
- Anum, F., Raja, N.I., Sultana, T., Kazmi, A., Ali, A., Qayyum, B., Afzal, A., Nijibat, A. & Mashwani, Z.U.R. (2021) Spectral lights based treatment enhanced biomass accumulation and secondary metabolites production in callus culture of *Citrus reticulata*. *The Philippine Agricultural Scientist*, 104(3), 287–298.
- Appolloni, E., Pennisi, G., Paucuk, I., Cellini, A., Crepaldi, A., Spinelli, F., Gianquinto, G., Gabarrell, X. & Orsini, F. (2023) Potential application of pre-harvest LED interlighting to improve tomato quality and storability. *Postharvest Biology and Technology*, 195, 112113. <https://doi.org/10.1016/j.postharvbio.2022.112113>
- Asad Ullah, M., Tungmunthum, D., Garros, L., Hano, C. & Abbasi, B.H. (2019) Monochromatic lights-induced trends in antioxidant and anti-diabetic polyphenol accumulation in vitro callus cultures of *Lepidium sativum* L. *Journal of Photochemistry and Photobiology B: Biology*, 196, 111505. <https://doi.org/10.1016/j.jphotobiol.2019.05.002>
- Ávalos-Sánchez, E., Moreno-Teruel, M.Á., Molina-Aiz, F.D., López-Martínez, A., Peña-Fernández, A., Baptista, F. & Valera-Martínez, D.L. (2022) Influence of the diffusivity and transmittance of a plastic greenhouse cover on the development of fungal diseases in a cucumber crop. *Agronomy*, 12(11), 2743. <https://doi.org/10.3390/agronomy12112743>
- Bajwa, M.N., Khanum, M., Zaman, G., Ullah, M.A., Farooq, U., Waqas, M., Ahmad, N., Hano, C. & Abbasi, B.H. (2023) Effect of wide-spectrum monochromatic lights on growth, phytochemistry, nutraceuticals, and antioxidant potential of in vitro callus cultures of *Moringa oleifera*. *Molecules*, 28(3), 1497. <https://doi.org/10.3390/molecules28031497>
- Baker, N.R. (2008) Chlorophyll fluorescence: a probe of photosynthesis in vivo. *Annual Review of Plant Biology*, 59, 89–113. <https://doi.org/10.1146/annurev.arplant.59.032607.092759>
- Basile, B., Giaccone, M., Cirillo, C., Ritieni, A., Graziani, G., Shahak, Y. & Forlani, M. (2012) Photo-selective hail nets affect fruit size and quality in Hayward kiwifruit. *Scientia Horticulturae*, 141, 91–97. <https://doi.org/10.1016/j.scienta.2012.04.022>
- Bastias, R.M., Manfrini, L. & Grappadelli, L.C. (2012) Exploring the potential use of photo-selective nets for fruit growth regulation in apple. *Chilean Journal of Agricultural Research*, 72(2), 224.
- Bennie, J., Davies, T.W., Cruse, D., Bell, F. & Gaston, K.J. (2017) Artificial light at night alters grassland vegetation species composition and phenology. *Journal of Applied Ecology*, 55(1), 442–450. <https://doi.org/10.1111/1365-2664.12927>
- Bennie, J., Davies, T.W., Cruse, D. & Gaston, K.J. (2016) Ecological effects of artificial light at night on wild plants. *Journal of Ecology*, 104(3), 611–620. <https://doi.org/10.1111/1365-2745.12551>
- Biswal, B., Jena, B., Giri, A.K. & Acharya, L. (2022) Monochromatic light elicited biomass accumulation, antioxidant activity, and secondary metabolite production in callus culture of *Operculina turpethum* (L.). *Plant Cell, Tissue and Organ Culture*, 149(1–2), 123–134. <https://doi.org/10.1007/s11240-022-02274-9>
- Björn, L.O. (Ed.) (2015) *Photobiology: The Science of Light and Life*. Springer New York, New York, NY. <https://doi.org/10.1007/978-1-4939-1468-5>
- Björn, L.O., Papageorgiou, G.C., Blankenship, R.E. & Govindjee (2009) A viewpoint: Why chlorophyll a? *Photosynthesis Research*, 99, 85–98. <https://doi.org/10.1007/s11220-008-9395-x>
- Bonanomi, G., Chirico, G.B., Palladino, M., Gaglione, S.A., Crispo, D.G., Lazzaro, U., Sica, B., Cesarano, G., Ippolito, F., Sarker, T.C., Rippa, M. & Scala, F. (2017) Combined application of photo-selective mulching films and beneficial microbes affects crop yield and irrigation water productivity in intensive farming systems. *Agricultural Water Management*, 184, 104–113. <https://doi.org/10.1016/j.agwat.2017.01.011>
- Bourget, C.M. (2008) An introduction to light-emitting diodes. *HortScience horts*, 43(7), 1944–1946. <https://doi.org/10.21273/HORTSCI.43.7.1944>
- Brodersen, C.R. & Vogelmann, T.C. (2010) Do changes in light direction affect absorption profiles in leaves?. *Functional Plant Biology*, 37(5), 403–412. <https://doi.org/10.1071/FP09262>
- Cabrera, J., Conesa, C.M. & Del Pozo, J.C. (2022) May the dark be with roots: a perspective on how root illumination may bias in vitro research on plant–environment interactions. *New Phytologist*, 233(5), 1988–1997. <https://doi.org/10.1111/nph.17936>
- Carillo, P., El-Nakhel, C., De Micco, V., Giordano, M., Pannico, A., De Pascale, S., Graziani, G., Ritieni, A., Soteriou, G.A., Kyriacou, M.C. & Roupheal, Y. (2022) Morpho-metric and specialized metabolites modulation of parsley microgreens through selective LED wavebands. *Agronomy*, 12(7), 1502. <https://doi.org/10.3390/agronomy12071502>
- Casal, J.J. (2000) Phytochromes, cryptochromes, phototropin: photoreceptor interactions in plants. *Photochemistry and Photobiology*, 71(1), 1–11.
- Casierra-Posada, F., Matallana-Díaz, Y.A. & Zapata-Casierra, E. (2014b) Growth of bell pepper plants (*Capsicum annuum*) affected by coloured covers. *Gesunde Pflanzen*, 66(4), 149–155. <https://doi.org/10.1007/s10343-014-0328-7>
- Casierra-Posada, F., Zapata-Casierra, E. & Chaparro-Chaparro, D.A. (2014a) Growth analysis in chard plants (*Beta vulgaris* L. Cicla, cv. 'Pencas Blancas') exposed to different light quality. *Agronomía Colombiana*, 32(2), 205–212. <https://doi.org/10.15446/agron.colomb.v32n2.42640>
- Cerny, T.A., Faust, J.E., Layne, D.R. & Rajapakse, N.C. (2003) Influence of photoselective films and growing season on stem growth and flowering of six plant species. *Journal of the American Society for Horticultural Science*, 128(4), 486–491. <https://doi.org/10.21273/JASHS.128.4.0486>
- Chaney, W.R. (2002) Does night lighting harm trees. *Purdue University, Forestry and Natural Resources, FAQ*, 17, 1–4.
- Chi, B., Zhang, X., Shi, Q., Wang, N. & Liu, Y. (2019). Colored plastic films affect demographic characteristics of *Aphis gossypii* on cucumber plants. *International Journal of Pest Management*, 65(4), 338–347. <https://doi.org/10.1080/09670874.2018.1522016>
- Chiocchio, I., Barbaresi, A., Barbanti, L., Mandrone, M., Poli, F., Torreggiani, D., Trenta, M. & Tassinari, P. (2022) Effects of LED supplemental lighting on the growth and metabolomic profile of *Taxus baccata* cultivated in a smart greenhouse. *PLoS ONE*, 17(7), e0266777. <https://doi.org/10.1371/journal.pone.0266777>
- Choi, H.G., Moon, B.Y. & Kang, N.J. (2015) Effects of LED light on the production of strawberry during cultivation in a plastic greenhouse and in a growth chamber. *Scientia Horticulturae*, 189, 22–31. <https://doi.org/10.1016/j.scienta.2015.03.022>
- Clifford, S.C., Runkle, E.S., Langton, F.A., Mead, A., Foster, S.A., Pearson, S. & Heins, R.D. (2004) Height control of poinsettia using photoselective filters. *HortScience*, 39(2), 383–387. <https://doi.org/10.21273/HORTSCI.39.2.383>
- Cozzolino, E., Di Mola, I., Ottaiano, L., El-Nakhel, C., Mormile, P., Roupheal, Y. & Mori, M. (2020). The potential of greenhouse diffusing cover material on yield and nutritive values of lamb's lettuce grown under diverse nitrogen regimes. *Italus Hortus*, 27(1), 55–67. <https://doi.org/10.4081/ija.2022.2061>
- Csizinszky, A.A., Schuster, D.J. & Kring, J.B. (1995) Color mulches influence yield and insect pest populations in tomatoes. *Journal of the American Society for Horticultural Science*, 120(5), 778–784.
- Czaja, M. & Koltun, A. (2022) How light pollution can affect spring development of urban trees and shrubs. *Urban Forestry & Urban Greening*, 77, 127753. <https://doi.org/10.1016/j.ufug.2022.127753>

- da Cunha Honorato, A., Nohara, G.A., de Assis, R.M.A., Maciel, J.F.A., de Carvalho, A.A., Pinto, J.E.B.P. & Bertolucci, S.K.V. (2023) Colored shade nets and different harvest times alter the growth, antioxidant status, and quantitative attributes of glandular trichomes and essential oil of *Thymus vulgaris* L. *Journal of Applied Research on Medicinal and Aromatic Plants*, 35(May), 100474 <https://doi.org/10.1016/j.jarmap.2023.100474>
- Danziger, N. & Bernstein, N. (2021) Light matters: Effect of light spectra on cannabinoid profile and plant development of medical cannabis (*Cannabis sativa* L.). *Industrial Crops and Products*, 164, 113351. <https://doi.org/10.1016/j.indcrop.2021.113351>
- de Freitas, I.S., Roldán, G.Q., Macedo, A.C. & Mello, S.D.C. (2021) The responses of photosynthesis, fruit yield and quality of mini-cucumber to LED-interlighting and grafting. *Horticultura Brasileira*, 39, 86–93. <https://doi.org/10.1590/s0102-0536-20210113>
- Díaz-Pérez, J.C. & Batal, K.D. (2002) Colored plastic film mulches affect tomato growth and yield via changes in root-zone temperature. *Journal of the American Society for Horticultural Science*, 127(1), 127–135. <https://doi.org/10.21273/JASHS.127.1.127>
- Dougher, T.A. & Bugbee, B. (2007) Evidence for yellow light suppression of lettuce growth. *Photochemistry and Photobiology*, 73(2), 208–212. [https://doi.org/10.1562/0031-8655\(2001\)0730208Befylso2.0.co2](https://doi.org/10.1562/0031-8655(2001)0730208Befylso2.0.co2)
- Doukas, D. & Payne, C.C. (2014) Greenhouse whitefly (Homoptera: Aleyrodidae) dispersal under different UV-light environments. *Journal of Economic Entomology*, 100(2), 389–397. <https://doi.org/10.1093/jee/100.2.389>
- Eftekhari, M., Javid, M.G., Aliniaefard, S. & Nicola, S. (2023) Alteration of flower yield and phytochemical compounds of saffron (*Crocus sativus* L.) by application of different light qualities and growth regulators. *Horticulturae*, 9(2), 169. <https://doi.org/10.3390/horticulturae9020169>
- El-Bashir, S.M., Al-Harbi, F.F., Elburaih, H., Al-Faifi, F. & Yahia, I.S. (2016). Red photoluminescent PMMA nanohybrid films for modifying the spectral distribution of solar radiation inside greenhouses. *Renewable Energy*, 85, 928–938. <https://doi.org/10.1016/j.renene.2015.07.031>
- Falciatore, A. & Bowler, C. (2005) The evolution and function of blue and red light photoreceptors. *Current Topics in Developmental Biology*, 68, 317–350. [https://doi.org/10.1016/S0070-2153\(05\)68011-8](https://doi.org/10.1016/S0070-2153(05)68011-8)
- Ffrench-Constant, R.H., Somers-Yeates, R., Bennie, J., Economou, T., Hodgson, D., Spalding, A. & McGregor, P.K. (2016) Light pollution is associated with earlier tree budburst across the United Kingdom. *Proceedings of the Royal Society B*, 283, 20160813. <https://doi.org/10.1098/rspb.2016.0813>
- Fitzmorris, B.C., Pu, Y.C., Cooper, J.K., Lin, Y.F., Hsu, Y.J., Li, Y. & Zhang, J.Z. (2013) Optical Properties and Exciton Dynamics of Alloyed Core/Shell/Shell Cd_{1-x}Zn_xSe/ZnSe/ZnS Quantum Dots. *ACS Applied Materials & Interfaces*, 5(8), 2893–2900. <https://doi.org/10.1021/am303149r>
- Fletcher, J.M., Tasiopoulou, A., Mpezamihigo, M., Carew, J.G., Henbest, R.G.C. & Hadley, P. (2005) Far-red light filtering by plastic film, greenhouse-cladding materials: effects on growth and flowering in Petunia and Impatiens. *The Journal of Horticultural Science and Biotechnology*, 80(3), 303–306. <https://doi.org/10.1080/14620316.2005.11511934>
- Folta, K.M. & Carvalho, S.D. (2015) Photoreceptors and control of horticultural plant traits. *HortScience horts*, 50(9), 1274–280. <https://doi.org/10.21273/HORTSCI.50.9.1274>
- Folta, K.M. & Maruhnich, S.A. (2007) Green light: a signal to slow down or stop. *Journal of Experimental Botany*, 58(12), 3099–3111. <https://doi.org/10.1093/jxb/erm130>
- Frechilla, S., Talbott, L.D., Bogomolni, R.A. & Zeiger, E. (2000) Reversal of blue light-stimulated stomatal opening by green light. *Plant Cell Physiology*, 41, 171–176. <https://doi.org/10.1093/pcp/41.2.171>
- Gao, S., Liu, X., Liu, Y., Cao, B., Chen, Z. & Xu, K. (2021) The spectral irradiance, growth, photosynthetic characteristics, antioxidant system, and nutritional status of green onion (*Allium fistulosum* L.) grown under different photo-selective nets. *Frontiers in Plant Science*, 12, 650471. <https://doi.org/10.3389/fpls.2021.650471>
- Gao, Y., Li, G., Cai, B., Zhang, Z., Li, N., Liu, Y. & Li, Q. (2022) Effects of rare-earth light conversion film on the growth and fruit quality of sweet pepper in a solar greenhouse. *Frontiers in Plant Science*, 13, 989271. <https://doi.org/10.3389/fpls.2022.989271>
- González, A., Rodríguez, R., Bañón, S., Franco, J.A., Fernández, J.A., Salmerón, A. & Espí, E. (2003) Strawberry and cucumber cultivation under fluorescent photosensitive plastic films cover. *Acta Horticulturae*, 614, 407–413. <https://doi.org/10.17660/ActaHortic.2003.614.61>
- González, C.V., Fanzone, M.L., Cortés, L.E., Bottini, R., Lijavetzky, D.C., Ballaré, C.L. & Bocalandro, H.E. (2015) Fruit-localized photoreceptors increase phenolic compounds in berry skins of field-grown *Vitis vinifera* L. cv. *Malbec*. *Phytochemistry*, 110, 46–57. <https://doi.org/10.1016/j.phytochem.2014.11.018>
- Gudkov, S.V., Simakin, A.V., Bunkin, N.F., Shafeev, G.A., Astashev, M.E., Glinushkin, A.P., Grinberg, M.A. & Vodenev, V.A. (2020) Development and application of photoconversion fluoropolymer films for greenhouses located at high or polar latitudes. *Journal of Photochemistry and Photobiology B: Biology*, 213(October), 112056. <https://doi.org/10.1016/j.jphotobiol.2020.112056>
- Han, X., Tohge, T., Lalor, P., Dockery, P., Devaney, N., Esteves-Ferreira, A.A., Fernie, A.R. & Sulpice, R. (2017) Phytochrome A and B regulate primary metabolism in *Arabidopsis* leaves in response to light. *Frontiers in Plant Science*, 8, 1394. <https://doi.org/10.3389/fpls.2017.01394>
- He, R., Wei, J., Zhang, J., Tan, X., Li, Y., Gao, M. & Liu, H. (2022) Supplemental blue light frequencies improve ripening and nutritional qualities of tomato fruits. *Frontiers in Plant Science*, 13, 888976. <https://doi.org/10.3389/fpls.2022.888976>
- Hemming, S.O.E.A., Van Os, E.A., Hemming, J. & Dieleman, J.A. (2006) The effect of new developed fluorescent greenhouse films on the growth of *Fragaria x ananassa* 'Elsanta'. *European Journal of Horticultural Science*, 71(4), 145–154.
- Holcman, E., Sentelhas, P.C. & Mello, S.D.C. (2015) Microclimatic changes caused by different plastic coverings in greenhouses cultivated with cherry tomato in southern Brazil. *Revista Brasileira de Meteorologia*, 30, 125–133. <https://doi.org/10.1590/0102-778620140094>
- Hölker, F., Moss, T., Griefahn, B., Kloas, W., Voigt, C.C., Henckel, D., Hänel, A., Kappeler, P.M., Völker, S., Schwöpe, A., Franke, S., Uhrlandt, D., Fisher, J., Klenke, R., Wolter, C. & Tockner, K. (2010) The dark side of light: a transdisciplinary research agenda for light pollution policy. *Ecology and Society*, 15(4). <http://www.ecologyandsociety.org/vol15/iss4/art13/>
- 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>
- Horrer, D., Flüttsch, S., Pazmino, D., Matthews, J.S., Thalmann, M., Nigro, A., Leonhardt, N., Lawson, T. & Santelia, D. (2016) Blue light induces a distinct starch degradation pathway in guard cells for stomatal opening. *Current Biology*, 26(3), 362–370. <https://doi.org/10.1016/j.cub.2015.12.036>
- Ilić, Z.S., Milenković, L., Šunić, L., Barać, S., Mastilović, J., Kevrešan, Ž. & Fallik, E. (2017) Effect of shading by coloured nets on yield and fruit quality of sweet pepper. *Zemdirbyste-Agriculture*, 104(1), 53–62. <https://doi.org/10.13080/z-a.2017.104.008>
- Izzo, L.G., Mickens, M.A., Aronne, G. & Gómez, C. (2021) Spectral effects of blue and red light on growth, anatomy, and physiology of lettuce. *Physiologia Plantarum*, 172(4), 2191–2202. <https://doi.org/10.1111/ppl.13395>
- Jensen, N.B., Clausen, M.R. & Kjaer, K.H. (2018) Spectral quality of supplemental LED grow light permanently alters stomatal functioning and

- chilling tolerance in basil (*Ocimum basilicum* L.). *Scientia Horticulturae*, 227, 38–47. <https://doi.org/10.1016/j.scienta.2017.09.011>
- Johkan, M., Shoji, K., Goto, F., Hahida, S.N. & Yoshihara, T. (2012) Effect of green light wavelength and intensity on photomorphogenesis and photosynthesis in *Lactuca sativa*. *Environmental and Experimental Botany*, 75, 128–133. <https://doi.org/10.1016/j.envexpbot.2011.08.010>
- Jokar, A., Zare, H., Zakerin, A. & Jahromi, A.A. (2021) The influence of photo-selective netting on tree physiology and fruit quality of fig (*Ficus carica* L.) under rain-fed conditions. *International Journal of Fruit Science*, 21(1), 896–910. <https://doi.org/10.1080/15538362.2021.1936345>
- Jones, M.A. (2018) Using light to improve commercial value. *Horticulture Research*, 5, 47. <https://doi.org/10.1038/s41438-018-0049-7>
- Junttila, O., Nilsen, J. & Igeland, B. (2003) Effect of temperature on the induction of bud dormancy in ecotypes of *Betula pubescens* and *Betula pendula*. *Scandinavian Journal of Forest Research*, 18(3), 208–217. <https://doi.org/10.1080/02827581.2003.9728291>
- Kaiser, E., Ouzounis, T., Giday, H., Schipper, R., Heuvelink, E. & Marcelis, L.F. (2019) Adding blue to red supplemental light increases biomass and yield of greenhouse-grown tomatoes, but only to an optimum. *Frontiers in Plant Science*, 9, 2002. <https://doi.org/10.3389/fpls.2018.02002>
- Kalaitzoglou, P., Taylor, C., Calders, K., Hogervorst, M., van Ieperen, W., Harbinson, J., de Visser, P., Nicole, C.C.S. & Marcelis, L.F.M. (2021) Unraveling the effects of blue light in an artificial solar background light on growth of tomato plants. *Environmental and Experimental Botany*, 184, 104377. <https://doi.org/10.1016/j.envexpbot.2021.104377>
- Kang, J.S., Kang, J.G., Sohn, Y. & Leung, K.T. (2018) Blue-light-emitting photostable hybrid films for high-efficiency large-area light converter and photonic applications. *ACS Applied Materials and Interfaces*, 10(51), 44768–44775. <https://doi.org/10.1021/acsami.8b17256>
- Khattak, A.M. & Pearson, S. (2006) Spectral filters and temperature effects on the growth and development of chrysanthemums under low light integral. *Plant Growth Regulation*, 49, 61–68. <https://doi.org/10.1007/s10725-006-0020-8>
- Khurshid, R., Ullah, M.A., Tungmunthum, D., Drouet, S., Shah, M., Zaeem, A., Hameed, S., Hano, C. & Abbasi, B.H. (2020) Lights triggered differential accumulation of antioxidant and antidiabetic secondary metabolites in callus culture of *Eclipta alba* L. *PLoS ONE*, 15(6), e0233963. <https://doi.org/10.1371/journal.pone.0233963>
- Kim, D. & Son, J.E. (2022) Adding far-red to red, blue supplemental light-emitting diode interlighting improved sweet pepper yield but attenuated carotenoid content. *Frontiers in Plant Science*, 13, 938199. <https://doi.org/10.3389/fpls.2022.938199>
- Kim, H.H., Goins, G.D., Wheeler, R.M. & Sager, J.C. (2004) Stomatal conductance of lettuce grown under or exposed to different light quality. *Annals of Botany*, 94(5), 691–697. <https://doi.org/10.1093/aob/mch192>
- Kim, Y.J., Kim, H.M., Kim, H.M., Jeong, B.R., Lee, H.J., Kim, H.J. & Hwang, S.J. (2018) Ice plant growth and phytochemical concentrations are affected by light quality and intensity of monochromatic light-emitting diodes. *Horticulture, Environment, and Biotechnology*, 59, 529–536. <https://doi.org/10.1007/s13580-018-0058-3>
- Kitayama, M., Nguyen, D.T., Lu, N. & Takagaki, M. (2019) Effect of light quality on physiological disorder, growth, and secondary metabolite content of water spinach (*Ipomoea aquatica* forsk) cultivated in a closed-type plant production system. *Horticultural Science and Technology*, 37(2), 206–218. <https://doi.org/10.12972/kjst.20190020>
- Kitazaki, K., Fukushima, A., Nakabayashi, R., Okazaki, Y., Kobayashi, M., Mori, T., Nishizawa, T., Reyes-Chin-Wo, S., Michelmoro, R.W., Saito, K., Shoji, K. & Kusano, M. (2018) Metabolic reprogramming in leaf lettuce grown under different light quality and intensity conditions using narrow-band LEDs. *Scientific reports*, 8(1), 7914. <https://doi.org/10.1038/s41598-018-25686-0>
- Kittas, C., Tchamitchian, M., Katsoulas, N., Karaiskou, P. & Papaioannou, C. (2006) Effect of two UV-absorbing greenhouse-covering films on growth and yield of an eggplant soilless crop. *Scientia Horticulturae*, 110(1), 30–37. <https://doi.org/10.1016/j.scienta.2006.06.018>
- Kleemann, M. (2002) Effect of photosensitive plastics on the quality of lettuce. *Acta Horticulturae*, 633, 173–179. <https://doi.org/10.17660/ActaHortic.2004.633.21>
- Kobayashi, K. & Masuda, T. (2019) Transcriptional control for the chlorophyll metabolism. *Advances in Botanical Research*, 91, 133–161. <https://doi.org/10.1016/bs.abr.2019.03.001>
- Kobori, M.M.R.G., da Costa Mello, S., de Freitas, I.S., Silveira, F.F., Alves, M.C. & Azevedo, R.A. (2022) Supplemental light with different blue and red ratios in the physiology, yield and quality of *Impatiens*. *Scientia Horticulturae*, 306, 111424. <https://doi.org/10.1016/j.scienta.2022.111424>
- Kong, Y., Stasiak, M., Dixon, M.A. & Zheng, Y. (2018) Blue light associated with low phytochrome activity can promote elongation growth as shade-avoidance response: A comparison with red light in four bedding plant species. *Environmental and Experimental Botany*, 155, 345–359. <https://doi.org/10.1016/j.envexpbot.2018.07.021>
- Kong, Y. & Zheng, Y. (2020) Phototropin is partly involved in blue-light-mediated stem elongation, flower initiation, and leaf expansion: A comparison of phenotypic responses between wild *Arabidopsis* and its phototropin mutants. *Environmental and Experimental Botany*, 171, 103967. <https://doi.org/10.1016/j.envexpbot.2019.103967>
- Kumar, D., Singh, H., Raj, S. & Soni, V. (2020) Chlorophyll a fluorescence kinetics of mung bean (*Vigna radiata* L.) grown under artificial continuous light. *Biochemistry and Biophysics Reports*, 24, 100813. <https://doi.org/10.1016/j.bbrep.2020.100813>
- Kwak, M.J., Je, S.M., Cheng, H.C., Seo, S.M., Park, J.H., Baek, S.G., Khaine, I., Lee, T., Jang, J., Li, Y., Kim, H., Lee, J.K., Kim, J. & Woo, S.Y. (2018) Night light-adaptation strategies for photosynthetic apparatus in yellow-poplar (*Liriodendron tulipifera* L.) exposed to artificial night lighting. *Forests*, 9(2), 74. <https://doi.org/10.3390/f9020074>
- Kwak, M.J., Lee, S.H., Khaine, I., Je, S.M., Lee, T.Y., You, H.N., Lee, H.K., Jang, J.H., Kim, I. & Woo, S.Y. (2017) Stomatal movements depend on interactions between external night light cue and internal signals activated by rhythmic starch turnover and abscisic acid (ABA) levels at dawn and dusk. *Acta Physiologia Plantarum*, 39, 162. <https://doi.org/10.1007/s11738-017-2465-y>
- Landi, M., Agati, G., Fini, A., Guidi, L., Sebastiani, F. & Tattini, M. (2021) Unveiling the shade nature of cyanic leaves: A view from the “blue absorbing side” of anthocyanins. *Plant, Cell & Environment*, 44(4), 1119–1129. <https://doi.org/10.1111/pce.13818>
- Landi, M., Zivcak, M., Sytar, O., Brestic, M. & Allakhverdiev, S.I. (2020) Plasticity of photosynthetic processes and the accumulation of secondary metabolites in plants in response to monochromatic light environments: A review. *Biochimica et Biophysica Acta (BBA) - Bioenergetics*, 1861(2), 148131. <https://doi.org/10.1016/j.bbabi.2019.148131>
- Lara, O.A., Amorós, A., Tapia, M.L. & Escalona, V.H. (2021) Effect of a photosensitive filter on the yield and postharvest quality of ‘Viroflay’ baby spinach (*Spinacia oleracea* L.) leaves cultivated in a hydroponic system. *Scientia Horticulturae*, 277, 109804. <https://doi.org/10.1016/j.scienta.2020.109804>
- Lauria, G., Lo Piccolo, E., Ceccanti, C., Guidi, L., Bernardi, R., Araniti, F., Crottozzi, L., Pellegrini, E., Moriconi, M., Giordani, T., Pugliesi, C., Nali, C., Sanità di Toppi, L., Paoli, L., Malorgio, F., Vernieri, P., Massai, R., Remorini, D. & Landi, M. (2023a) Supplemental red LED light promotes plant productivity, “photomodulate” fruit quality and increases *Botrytis cinerea* tolerance in strawberry. *Postharvest Biology and Technology*, 198, 112253. <https://doi.org/10.1016/j.postharvbio.2023.112253>
- Lauria, G., Lo Piccolo, E., Davini, A., Castiglione, M.R., Pieracci, Y., Flamini, G., Martens, S., Angeli, A., Ceccanti, C., Guidi, L., Pellegrini, E., Incrocci, L. & Landi, M. (2023b) Modulation of VOC fingerprint and

- alteration of physiological responses after supplemental LED light in green-and red-leafed sweet basil (*Ocimum basilicum* L.). *Scientia Horticulturae*, 315, 111970. <https://doi.org/10.1016/j.scienta.2023.111970>
- Lauria, G., Lo Piccolo, E., Pellegrini, E., Bellini, E., Giordani, T., Guidi, L., Lorenzini, G., Malorgio, F., Massai, R., Nali, C., Paoli, L., Remorini, D., Sanità di Toppi, L., Vernieri, P. & Landi, M. (2021) Photosynthetic traits and biochemical responses in strawberry (*Fragaria* × *ananassa* Duch.) leaves supplemented with LED lights. *Photosynthetica*, 59(4), 557–569. <https://doi.org/10.32615/ps.2021.048>
- Lauria, G., Lo Piccolo, E., Ceccanti, C., Paoli, L., Giordani, T., Guidi, L., Malorgio, F., Massai, R., Nali, C., Pellegrini, E., Remorini, D., Sanità di Toppi, L., Vernieri, P. & Landi, M. (2023c) Supplemental red light more than other wavebands activates antioxidant defenses in greenhouse-cultivated *Fragaria* × *ananassa* var. *Elsanta* plants. *Scientia Horticulturae*, 321, 112319. <https://doi.org/10.1016/j.scienta.2023.112319>
- Li, C., Junttila, O., Ernstsén, A., Heino, P. & Palva, E.T. (2003b) Photoperiodic control of growth, cold acclimation and dormancy development in silver birch (*Betula pendula*) ecotypes. *Physiologia Plantarum*, 117(2), 206–212. <https://doi.org/10.1034/j.1399-3054.2003.00002.x>
- Li, J., Zhangzhong, L., Zhang, X., Wei, X., Zhang, S., Wang, L. & Zheng, W. (2022) Effects of light conversion film on the growth of leafy vegetables in facilities under haze weather. *Agronomy*, 12, 2391. <https://doi.org/10.3390/agronomy12102391>
- Li, S., Rajapakse, N.C. & Young, R.E. (2003a) Far-red light absorbing photo-selective plastic films affect growth and flowering of chrysanthemum cultivars. *HortScience*, 38(2), 284–287. <https://doi.org/10.21273/HORTSCI.38.2.284>
- Li, S., Rajapakse, N.C., Young, R.E. & Oi, R. (2000) Growth responses of chrysanthemum and bell pepper transplants to photosensitive plastic films. *Scientia Horticulturae*, 84(3–4), 215–225. [https://doi.org/10.1016/S0304-4238\(99\)00136-3](https://doi.org/10.1016/S0304-4238(99)00136-3)
- Li, X.T., Chen, B., Wang, H.J., Zheng, G., Yang, D., Miao, X.Y. & Xu, C. (2019) Effects of urban nighttime light on the growth of *Cinnamomum camphora*. *Ying Yong Sheng Tai Xue Bao*, 30, 2284–2290. <https://doi.org/10.13287/j.1001-9332.201907.009>
- Lian, X., Jiao, L., Zhong, J., Jia, Q., Liu, J. & Liu, Z. (2021) Artificial light pollution inhibits plant phenology advance induced by climate warming. *Environmental Pollution*, 291, 118110. <https://doi.org/10.1016/j.envpol.2021.118110>
- Lichtenthaler, H.K. (1996) Vegetation stress: an introduction to the stress concept in plants. *Journal of Plant Physiology*, 148(1–2), 4–14. [https://doi.org/10.1016/S0176-1617\(96\)80287-2](https://doi.org/10.1016/S0176-1617(96)80287-2)
- Lin, C. (2000) Photoreceptors and regulation of flowering time. *Plant Physiology*, 123, 39–50. <https://doi.org/10.1104/pp.123.1.39>
- Liu, P., Cao, B., Wang, Y., Wei, Z., Ye, J. & Wei, H. (2021) Spectral effect of streetlamps on urban trees: A simulated study on tissue water, nitrogen, and carbohydrate contents in maple and oak. *PLoS ONE*, 16(3), e0248463. <https://doi.org/10.1371/journal.pone.0248463>
- Liu, Y., Gui, Z. & Liu, J. (2022) Research progress of light wavelength conversion materials and their applications in functional agricultural films. *Polymers*, 14(5), 851. <https://doi.org/10.3390/polym14050851>
- Lo Piccolo, E., Lauria, G., Guidi, L., Remorini, D., Massai, R. & Landi, M. (2023) Shedding light on the effects of LED streetlamps on trees in urban areas: Friends or foes?. *Science of the Total Environment*, 865, 161200. <https://doi.org/10.1016/j.scitotenv.2022.161200>
- Lo Piccolo, E., Lauria, G., Remorini, D., Massai, R., Guidi, L. & Landi, M. (2021) Urban lighting alters chlorophyll metabolism and promotes CO₂ assimilation during the night in *Tilia plathyphyllos* Scop. and *Platanus x acerifolia* (Aiton) Willd. *Agrochimica*, 65(4), 389–400. <https://doi.org/10.12871/00021857202146>
- Lo Piccolo, E., Torre, S., Lauria, G., De Quattro, C., Sebastiani, F., Guidi, L., Remorini, D., Massai, R. & Landi, M. (2024) LED streetlamps alter tree architecture, downregulate the photosynthetic process and alter the sugar metabolism of *Populus alba* L. *Environmental and Experimental Botany*, 226, 105861. <https://doi.org/10.1016/j.envenxpbot.2024.105861>
- Lobiuc, A., Vasilache, V., Pintilie, O., Stoleru, T., Burducea, M., Oroian, M. & Zamfirache, M.-M. (2017) Blue and red LED illumination improves growth and bioactive compounds contents in acyanic and cyanic *Ocimum basilicum* L. microgreens. *Molecules*, 22, 2111. <https://doi.org/10.3390/molecules22122111>
- Lobos, G.A., Retamales, J.B., Hancock, J.F., Flore, J.A., Romero-Bravo, S. & Del Pozo, A. (2013) Productivity and fruit quality of *Vaccinium corymbosum* cv. Elliott under photo-selective shading nets. *Scientia Horticulturae*, 153, 143–149. <https://doi.org/10.1016/j.scienta.2013.02.012>
- Long, S.P., Zhu, X. G., Naidu, S.L. & Ort, D.R. (2006) Can improvement in photosynthesis increase crop yields? *Plant, Cell and Environment*, 29(3), 315–330. <https://doi.org/10.1111/j.1365-3040.2005.01493.x>
- Lykas, C., Kittas, C., Katsoulas, N. & Papafotiou, M. (2008) *Gardenia jasminoides* height control using a photosensitive polyethylene film. *HortScience*, 43(7), 2027–2033. <https://doi.org/10.21273/HORTSCI.43.7.2027>
- Lykas, C., Petsani, D., Kittas, C. & Papafotiou, M. (2005) Effect of a red to far red light filtering plastic film on growth of gardenia (*Gardenia jasminoides*). *Acta Horticulturae*, 711, 399–404. <https://doi.org/10.17660/ActaHortic.2006.711.56>
- Magar, Y.G., Ohyama, K., Noguchi, A., Amaki, W. & Furufuji, S. (2018, August) Effects of light quality during supplemental lighting on the flowering in an everbearing strawberry. *Acta Horticulturae*, 1206, 279–284. <https://doi.org/10.17660/ActaHortic.2018.1206.39>
- Maki, S.L., Rajapakse, S., Ballard, R.E. & Rajapakse, N.C. (2002) Role of gibberellins in chrysanthemum growth under far red light-deficient greenhouse environments. *Journal of the American Society for Horticultural Science*, 127(4), 639–643. <https://doi.org/10.21273/JASHS.127.4.639>
- Manja, K. & Aoun, M. (2019) The use of nets for tree fruit crops and their impact on the production: A review. *Scientia Horticulturae*, 246, 110–122. <https://doi.org/10.1016/j.scienta.2018.10.050>
- Marigliano, L.E., Yu, R., Torres, N., Tanner, J.D., Battany, M. & Kurtural, S.K. (2022) Photosensitive shade films mitigate heat wave damage by reducing anthocyanin and flavonol degradation in grapevine (*Vitis vinifera* L.) berries. *Frontiers in Agronomy*, 4, 898870. <https://doi.org/10.3389/fagro.2022.898870>
- Massetti, L. (2018) Assessing the impact of street lighting on *Platanus x acerifolia* phenology. *Urban Forestry & Urban Greening*, 34, 71–77. <https://doi.org/10.1016/j.ufug.2018.05.015>
- Mathews, S. (2006) Phytochrome-mediated development in land plants: red light sensing evolves to meet the challenges of changing light environments. *Molecular Ecology*, 15(12), 3483–3503. <https://doi.org/10.1111/j.1365-294X.2006.03051.x>
- Matsuda, R., Ohashi-Kaneko, K., Fujiwara, K., Goto, E. & Kurata, K. (2004) Photosynthetic characteristics of rice leaves grown under red light with or without supplemental blue light. *Plant and Cell Physiology*, 45(12), 1870–1874. <https://doi.org/10.1093/pcp/pch203>
- Matthews, J.S., Violet-Chabrand, S. & Lawson, T. (2020). Role of blue and red light in stomatal dynamic behaviour. *Journal of Experimental Botany*, 71(7), 2253–2269. <https://doi.org/10.1093/jxb/erz563>
- Matysiak, B. (2021) The Effect of supplementary LED lighting on the morphological and physiological traits of Miniature *Rosa* × *Hybrida* ‘Aga’ and the development of Powdery Mildew (*Podosphaera pannosa*) under greenhouse conditions. *Plants*, 10(2), 417. <https://doi.org/10.3390/plants10020417>
- Matysiak, B. & Kowalski, A. (2019) White, blue and red LED lighting on growth, morphology and accumulation of flavonoid compounds in leafy greens. *Zemdirbyste-Agriculture*, 106(3), 281–286. <https://doi.org/10.13080/z-a.2019.106.036>
- Matzke, E.B. (1936) The effect of street lights in delaying leaf-fall in certain trees. *American Journal of Botany*, 23(6), 446–452. <https://www.jstor.org/stable/2436035>
- Mickens, M.A., Skoog, E.J., Reese, L.E., Barnwell, P.L., Spencer, L.E., Massa, G.D. & Wheeler, R.M. (2018) A strategic approach for

- investigating light recipes for 'Outredgeous' red romaine lettuce using white and monochromatic LEDs. *Life Sciences in Space Research*, 19, 53–62. <https://doi.org/10.1016/j.lssr.2018.09.003>
- Moradi, S., Kafi, M., Aliniaefard, S., Moosavi-Nezhad, M., Pedersen, C., Gruda, N.S. & Salami, S.A. (2022) Monochromatic blue light enhances crocin and picrocrocin content by upregulating the expression of underlying biosynthetic pathway genes in saffron (*Crocus sativus* L.). *Frontiers in Horticulture*, 1, 960423. <https://doi.org/10.3389/ehort.2022.960423>
- Morello, V., Brousseau, V.D., Wu, N., Wu, B.S., MacPherson, S. & Lefsrud, M. (2022). Light quality impacts vertical growth rate, phytochemical yield and cannabinoid production efficiency in *Cannabis sativa*. *Plants*, 11(21), 2982. <https://doi.org/10.3390/plants11212982>
- Moreno-Teruel, M. de los Á., Molina-Aiz, F.D., Peña-Fernández, A., López-Martínez, A. & Valera-Martínez, D.L. (2021) The effect of diffuse film covers on microclimate and growth and production of tomato (*Solanum lycopersicum* L.) in a Mediterranean greenhouse. *Agronomy*, 11(5). <https://doi.org/10.3390/agronomy11050860>
- Morrow, R.C. (2008) LED lighting in horticulture. *HortScience*, 43(7), 1947–1950. <https://doi.org/10.21273/HORTSCI.43.7.1947>
- Muneer, S., Kim, E.J., Park, J.S. & Lee, J.H. (2014) Influence of green, red and blue light emitting diodes on multiprotein complex proteins and photosynthetic activity under different light intensities in lettuce leaves (*Lactuca sativa* L.). *International Journal of Molecular Sciences*, 15(3), 4657–4670. <https://doi.org/10.3390/ijms15034657>
- Mupambi, G., Musacchi, S., Serra, S., Kalcsits, L.A., Layne, D.R. & Schmidt, T. (2018) Protective netting improves leaf-level photosynthetic light use efficiency in 'Honeycrisp' apple under heat stress. *HortScience*, 53(10), 1416–1422. <https://doi.org/10.21273/HORTSCI13096-18>
- Naureen, Z., Sham, A., Al Ashram, H., Gilani, S.A., Al Gheilani, S., Mabood, F., Hussain, J., Al Harrasi, A. & AbuQamar, S.F. (2018) Effect of phosphate nutrition on growth, physiology and phosphate transporter expression of cucumber seedlings. *Plant Physiology and Biochemistry*, 127, 211–222. <https://doi.org/10.1016/j.plaphy.2018.03.028>
- Nguyen, D.T., Kitayama, M., Lu, N. & Takagaki, M. (2020) Improving secondary metabolite accumulation, mineral content, and growth of coriander (*Coriandrum sativum* L.) by regulating light quality in a plant factory. *The Journal of Horticultural Science and Biotechnology*, 95(3), 356–363. <https://doi.org/10.1080/14620316.2019.1677510>
- Nishimura, Y., Wada, E., Fukumoto, Y., Aruga, H. & Shimoi, Y. (2012) The effect of spectrum conversion covering film on cucumber in soilless culture. *Acta Horticulturae*, 956, 481–487. <https://doi.org/10.17660/ActaHortic.2012.956.56>
- Oliveira, G.C., Vieira, W.L., Bertolli, S.C. & Pacheco, A.C. (2016) Photosynthetic behavior, growth and essential oil production of *Melissa officinalis* L. cultivated under colored shade nets. *Chilean Journal of Agricultural Research*, 76(1), 123–128. <https://doi.org/10.4067/S0718-58392016000100017>
- Ooyama, H.E., Hayashi, A., Mamura, T., Ide, T., Hino, T., Tanigami, T. & Yoshida, K. (2012) Photophysical properties and photostability of novel unsymmetric polycyclicphenazine-type D- π -A fluorescent dyes and the dye-doped films. *Journal of Photochemistry and Photobiology A: Chemistry*, 230(1), 38–46. <https://doi.org/10.1016/j.jphotochem.2011.12.009>
- Orlando, M., Trivellini, A., Incrocci, L., Ferrante, A. & Mensuali, A. (2022) The inclusion of green light in a red and blue light background impact the growth and functional quality of vegetable and flower microgreen species. *Horticulturae*, 8(3), 217. <https://doi.org/10.3390/horticulturae8030217>
- Papaioannou, C., Katsoulas, N., Maletsika, P., Siomos, A. & Kittas, C. (2012) Effects of a UV-absorbing greenhouse covering film on tomato yield and quality. *Spanish Journal of Agricultural Research*, 10(4), 959. <https://doi.org/10.5424/sjar/2012104-2899>
- Patil, R.T., Patil, B.C., Seetharamu, G.K., Mukund Shiragur, S., Nishani, R.S. & Mahantesha, N.B.N. (2020). Influence of photoselective shade nets on growth and yield of Asparagus. *International Journal of Chemical Studies*, 8(6), 2525–2528. <https://doi.org/10.22271/chemi.2020.v8.i6aj.11151>
- Pedroso, R.C.N., Branquinho, N.A.A., Hara, A.C., Costa, A.C., Silva, F.G., Pimenta, L. P., Silva, M.L.A., Cunha, W.R., Pauletti, P.M. & Janeiro, A.H. (2017) Impact of light quality on flavonoid production and growth of *Hyptis marrubioides* seedlings cultivated in vitro. *Revista Brasileira de Farmacognosia*, 27, 466–470. <https://doi.org/10.1016/j.bjp.2016.12.004>
- Petropoulos, S.A., Fernandes, Á., Katsoulas, N., Barros, L. & Ferreira, I.C.F. R. (2019) The effect of covering material on the yield, quality and chemical composition of greenhouse-grown tomato fruit. *Journal of the Science of Food and Agriculture*, 99(6), 3057–3068. <https://doi.org/10.1002/jsfa.9519>
- Pu, Y.C., Chen, W.T., Fang, M.J., Chen, Y.L., Tsai, K.A., Lin, W.H. & Hsu, Y.J. (2018) Au–Cd1 – xZnScore–alloyed shell nanocrystals: boosting the interfacial charge dynamics by adjusting the shell composition. *Journal of Materials Chemistry A*, 6(36), 17503–17513. <https://doi.org/10.1039/C8TA05539D>
- Puccinelli, M., Maggini, R., Angelini, L.G., Santin, M., Landi, M., Tavarini, S., Castagna, A. & Incrocci, L. (2022) Can light spectrum composition increase growth and nutritional quality of *Linum usitatissimum* L. sprouts and microgreens?. *Horticulturae*, 8(2), 98. <https://doi.org/10.3390/horticulturae8020098>
- Rai, N., Morales, L.O. & Aphalo, P.J. (2021) Perception of solar UV radiation by plants: photoreceptors and mechanisms. *Plant Physiology*, 186(3), 1382–1396. <https://doi.org/10.1093/plphys/kiab162>
- Riga, P. & Benedicto, L. (2017) Effects of light-diffusing plastic film on lettuce production and quality attributes. *Spanish Journal of Agricultural Research*, 15(1), 1–11. <https://doi.org/10.5424/sjar/2017151-10315>
- Rizzini, L., Favory, J.J., Cloix, C., Faggionato, D., O'hara, A., Kaiserli, E., Baumeister, R., Schafer, E., Nagy, F., Jenkins, G.I. & Ulm, R. (2011) Perception of UV-B by the Arabidopsis UVR8 protein. *Science*, 332(6025), 103–106. <https://doi.org/10.1126/science.1200660>
- Rong Sng, B.J., Mun, B., Mohanty, B., Kim, M., Phua, Z. W., Yang, H., Lee, D.Y. & Jang, I.C. (2021) Combination of red and blue light induces anthocyanin and other secondary metabolite biosynthesis pathways in an age-dependent manner in Batavia lettuce. *Plant Science*, 310, 110977. <https://doi.org/10.1016/j.plantsci.2021.110977>
- Rossi Pinheiro, R., Marques Pinheiro, M.V., Antonio Thiesen, L., Inês Diel, M., dos Santos, J., Otomar Caron, B. & Schmidt, D. (2020) The use of photoselective nets affects the leaf characteristics of lettuce cultivars. *Bulgarian Journal of Agricultural Science*, 26(4), 777–786.
- Runkle, E.S. & Heins, R.D. (2002) Stem extension and subsequent flowering of seedlings grown under a film creating a far-red deficient environment. *Scientia Horticulturae*, 96(1–4), 257–265. [https://doi.org/10.1016/S0304-4238\(02\)00055-9](https://doi.org/10.1016/S0304-4238(02)00055-9)
- Salazar-Canales, F., Bastías, R.M., Calderón-Orellana, A., Wilckens, R. & González, E. (2021) Photo-selective nets differentially affect microclimatic conditions, leaf physiological characteristics, and yield in hazelnut (*Corylus avellana* L.). *Horticulture, Environment, and Biotechnology*, 62(6), 845–858. <https://doi.org/10.1007/s13580-021-00365-8>
- Sanchez, F., Bassil, E., Crane, J.H., Shahid, M.A., Vincent, C.I. & Schaffer, B. (2022) Spectral light distribution affects photosynthesis, leaf reflective indices, antioxidant activity and growth of *Vanilla planifolia*. *Plant Physiology and Biochemistry*, 182, 145–153. <https://doi.org/10.1016/j.plaphy.2022.04.020>
- Sarabi, B., Ghaderi, N. & Ghashghaie, J. (2022) Light-emitting diode combined with humic acid improve the nutritional quality and enzyme activities of nitrate assimilation in rocket (*Eruca sativa* (Mill.) Thell.). *Plant Physiology and Biochemistry*, 187, 11–24. <https://doi.org/10.1016/j.plaphy.2022.07.035>

- Sarala, M., Tahkokorpi, M., Niinimaa, A., Laine, K., Taulavuori, E. & Taulavuori, K. (2013) Street lamp light does not delay autumnal leaf colouration of *Betula pendula*. *Trees*, 27, 1193–1199. <https://doi.org/10.1007/s00468-013-0841-9>
- Sathasivam, R., Park, S.U., Kim, J.K., Park, Y.J., Kim, M.C., Nguyen, B.V. & Lee, S.Y. (2023) Metabolic profiling of primary and secondary metabolites in kohlrabi (*Brassica oleracea* var. *gongylodes*) sprouts exposed to different light-emitting diodes. *Plants*, 12(6), 1296. <https://doi.org/10.3390/plants12061296>
- Seo, M., Hanada, A., Kuwahara, A., Endo, A., Okamoto, M., Yamauchi, Y., North, H., Marion-Poll, A., Sun, T.P., Koshiba, T., Kamiya, Y., Yamaguchi, S. & Nambara, E. (2006) Regulation of hormone metabolism in *Arabidopsis* seeds: phytochrome regulation of abscisic acid metabolism and abscisic acid regulation of gibberellin metabolism. *The Plant Journal*, 48, 354–366. <https://doi.org/10.1111/j.1365-313X.2006.02881.x>
- Shen, L., Lou, R., Park, Y., Guo, Y., Stallknecht, E.J., Xiao, Y., Rieder, D., Yang, R., Runkle, E.S. & Yin, X. (2021) Increasing greenhouse production by spectral-shifting and unidirectional light-extracting photonics. *Nature Food*, 2, 434–441. <https://doi.org/10.1038/s43016-021-00307-8>
- Shimazaki, K.I., Doi, M., Assmann, S.M. & Kinoshita, T. (2007) Light regulation of stomatal movement. *Annual Review of Plant Biology*, 58, 219–247. <https://doi.org/10.1146/annurev.arplant.57.032905.105434>
- Shiukhy, S., Raeini-Sarjaz, M. & Chalavi, V. (2015) Colored plastic mulch microclimates affect strawberry fruit yield and quality. *International Journal of Biometeorology*, 59(8), 1061–1066. <https://doi.org/10.1007/s00484-014-0919-0>
- Simkin, A.J., Kapoor, L., Doss, C.G.P., Hofmann, T.A., Lawson, T. & Ramamoorthy, S. (2022) The role of photosynthesis related pigments in light harvesting, photoprotection and enhancement of photosynthetic yield in planta. *Photosynthesis Research*, 152(1), 23–42. <https://doi.org/10.1007/s11120-021-00892-6>
- Singh, D., Basu, C., Meinhardt-Wollweber, M. & Roth, B. (2015) LEDs for energy efficient greenhouse lighting. *Renewable and Sustainable Energy Reviews*, 49, 139–147. <https://doi.org/10.1016/j.rser.2015.04.117>
- Škvareninová, J., Tuhárska, M., Škvarenina, J., Babálová, D., Slobodníková, L., Slobodník, B., Středová, H. & Minďaš, J. (2017) Effects of light pollution on tree phenology in the urban environment. *Moravian Geographical Reports*, 25(4), 282–290. <https://doi.org/10.1515/mgr-2017-0024>
- Stagnari, F., Di Mattia, C., Galieni, A., Santarelli, V., D'Egidio, S., Pagnani, G. & Pisante, M. (2018) Light quantity and quality supplies sharply affect growth, morphological, physiological and quality traits of basil. *Industrial Crops and Products*, 122, 277–289. <https://doi.org/10.1016/j.indcrop.2018.05.073>
- Stagnari, F., Galieni, A., Cafiero, G. & Pisante, M. (2014) Application of photo-selective films to manipulate wavelength of transmitted radiation and photosynthate composition in red beet (*Beta vulgaris* var. *conditiva* Alef.). *Journal of the Science of Food and Agriculture*, 94(4), 713–720. <https://doi.org/10.1002/jsfa.6312>
- Stamford, J.D., Stevens, J., Mullineaux, P.M. & Lawson, T. (2023) LED lighting: a grower's guide to light spectra. *HortScience*, 58(2), 180–196. <https://doi.org/10.21273/HORTSCI16823-22>
- Stapel, J.O., Maugin, E., Trihan, S. & Ferre, A. (2011) Light filter use in ornamental plant production to control plant growth and to improve plant quality. *Acta Horticulturae*, 907, 205–211. <https://doi.org/10.17660/ActaHortic.2011.907.30>
- Strasser, B., Sánchez-Lamas, M., Yanovsky, M.J., Casal, J.J. & Cerdán, P.D. (2010) *Arabidopsis thaliana* life without phytochromes. *Proceedings of the National Academy of Sciences*, 107(10), 4776–4781. <https://doi.org/10.1073/pnas.0910446107>
- Su, N., Wu, Q., Shen, Z., Xia, K. & Cui, J. (2014) Effects of light quality on the chloroplastic ultrastructure and photosynthetic characteristics of cucumber seedlings. *Plant Growth Regulation*, 73, 227–235. <https://doi.org/10.1007/s10725-013-9883-7>
- Su, P., Ding, S., Wang, D., Kan, W., Yuan, M., Chen, X., Tang, C., Hou, J. & Wu, L. (2024) Plant morphology, secondary metabolites and chlorophyll fluorescence of *Artemisia argyi* under different LED environments. *Photosynthesis Research*, 159, 153–164. <https://doi.org/10.1007/s11120-023-01026-w>
- Suzuki, J.Y. & Bauer, C.E. (1995) A prokaryotic origin for light-dependent chlorophyll biosynthesis of plants. *Proceedings of the National Academy of Sciences of the United States of America*, 92, 3749–3753. <https://doi.org/10.1073/pnas.92.9.3749>
- Szopa, A., Starzec, A. & Ekiert, H. (2018) The importance of monochromatic lights in the production of phenolic acids and flavonoids in shoot cultures of *Aronia melanocarpa*, *Aronia arbutifolia* and *Aronia × prunifolia*. *Journal of Photochemistry and Photobiology B: Biology*, 179, 91–97. <https://doi.org/10.1016/j.jphotobiol.2018.01.005>
- Takeda, F., Glenn, D.M., Callahan, A., Slovins, J. & Stutte, G.W. (2010) Delaying flowering in short-day strawberry transplants with photosensitive nets. *International Journal of Fruit Science*, 10(2), 134–142. <https://doi.org/10.1080/15538362.2010.492331>
- Tariq, U., Ali, M. & Abbasi, B.H. (2014) Morphogenic and biochemical variations under different spectral lights in callus cultures of *Artemisia absinthium* L. *Journal of Photochemistry and Photobiology B: Biology*, 130, 264–271. <https://doi.org/10.1016/j.jphotobiol.2013.11.026>
- Taulavuori, K., Hyöky, V., Oksanen, J., Taulavuori, E. & Julkunen-Tiitto, R. (2016) Species-specific differences in synthesis of flavonoids and phenolic acids under increasing periods of enhanced blue light. *Environmental and Experimental Botany*, 121, 145–150. <https://doi.org/10.1016/j.envexpbot.2015.04.002>
- Thwe, A.A., Kim, Y.B., Li, X., Seo, J.M., Kim, S.J., Suzuki, T., Chung, S.O. & Park, S.U. (2014) Effects of light-emitting diodes on expression of phenylpropanoid biosynthetic genes and accumulation of phenylpropanoids in *Fagopyrum tataricum* sprouts. *Journal of Agricultural and Food Chemistry*, 62(21), 4839–4845. <https://doi.org/10.1021/jf501335q>
- Tsormpatsidis, E., Henbest, R.G.C., Davis, F.J., Battey, N.H., Hadley, P. & Wagstaffe, A. (2008) UV irradiance as a major influence on growth, development and secondary products of commercial importance in Lollo Rosso lettuce 'Revolution' grown under polyethylene films. *Environmental and Experimental Botany*, 63(1–3), 232–239. <https://doi.org/10.1016/j.envexpbot.2007.12.002>
- Tuhárska, M., Krnáčková, D., Škvareninová, J. & Hříbik, M. (2014) Intensity of light pollution and its impact on phenological phases of trees. *Mendel a bioklimatologie*.
- Usman, H., Ullah, M.A., Jan, H., Siddiquah, A., Drouet, S., Anjum, S., Giglioli-Guviarc'h, N., Hano, C. & Abbasi, B.H. (2020) Interactive effects of wide-spectrum monochromatic lights on phytochemical production, antioxidant and biological activities of *Solanum xanthocarpum* callus cultures. *Molecules*, 25(9), 2201. <https://doi.org/10.3390/molecules25092201>
- Violet-Chabrand, S., Matthews, J.S. & Lawson, T. (2021) Light, power, action! Interaction of respiratory energy-and blue light-induced stomatal movements. *New Phytologist*, 231(6), 2231–2246. <https://doi.org/10.1111/nph.17538>
- Wang, L., Chen, J., Zhao, C., Jin, H., Li, F. & Wu, S. (2023) Production and quality of Hami melon (*Cucumis melo* var. *reticulatus*) and pest population of *Thrips palmi* in UV-blocking film greenhouses. *Pest Management Science*, 79(10), 4011–4017. <https://doi.org/10.1002/ps.7597>
- Wang, Q. & Lin, C. (2020) Mechanisms of cryptochrome-mediated photoresponses in plants. *Annual Review of Plant Biology*, 71, 103–129. <https://doi.org/10.1146/annurev-arplant-050718-100300>
- Wang, S., Fang, H., Xie, J., Wu, Y., Tang, Z., Liu, Z., Lv, J. & Yu, J. (2021) Physiological responses of cucumber seedlings to different supplemental light duration of red and blue LED. *Frontiers in Plant Science*, 12, 709313. <https://doi.org/10.3389/fpls.2021.709313>

- Wang, S., Meng, X., Tang, Z., Wu, Y., Xiao, X., Zhang, G., Hu, L., Lyu, J. & Yu, J. (2022) Red and blue LED light supplementation in the morning pre-activates the photosynthetic system of tomato (*Solanum lycopersicum* L.) leaves and promotes plant growth. *Agronomy*, 12(4), 897. <https://doi.org/10.3390/agronomy12040897>
- Wang, W., Su, M., Li, H., Zeng, B., Chang, Q. & Lai, Z. (2018) Effects of supplemental lighting with different light qualities on growth and secondary metabolite content of *Anoectochilus roxburghii*. *PeerJ*, 6, e5274. <https://doi.org/10.7717/peerj.5274>
- Wei, X., Zhao, X., Long, S., Xiao, Q., Guo, Y., Qiu, C., Qiu, H. & Wang, Y. (2021) Wavelengths of LED light affect the growth and cannabidiol content in *Cannabis sativa* L. *Industrial Crops and Products*, 165, 113433. <https://doi.org/10.1016/j.indcrop.2021.113433>
- Wilson, S.B. & Rajapakse, N.C. (2001a) Growth control of lisianthus by photosensitive plastic films. *HortTechnology*, 11(4), 581–584. <https://doi.org/10.21273/HORTTECH.11.4.581>
- Wilson, S.B. & Rajapakse, N.C. (2001b) Growth regulation of sub-tropical perennials by photosensitive plastic films. *Journal of Environmental Horticulture*, 19(2), 65–68. <https://doi.org/10.24266/0738-2898-19.2.65>
- Wilson, S.B. & Rajapakse, N.C. (2001c) Use of photosensitive plastic films to control growth of three perennial salvias. *Journal of Applied Horticulture*, 3(2), 71–74.
- Yan, Z., Wang, C., Wang, L., Li, X., Wang, G. & Yang, Y. (2022) The combinations of white, blue, and UV-A light provided by supplementary light-emitting diodes promoted the quality of greenhouse-grown cucumber seedlings. *Agriculture*, 12(10), 1593. <https://doi.org/10.3390/agriculture12101593>
- Yang, L., Fanourakis, D., Tsaniklidis, G., Li, K., Yang, Q. & Li, T. (2021) Contrary to red, blue monochromatic light improves the bioactive compound content in broccoli sprouts. *Agronomy*, 11(11), 2139. <https://doi.org/10.3390/agronomy11112139>
- Zhang, G., Li, Z., Cheng, J., Cai, X., Cheng, F., Yang, Y. & Yan, Z. (2022b) Morphological and physiological traits of greenhouse-grown tomato seedlings as influenced by supplemental white plus red versus red plus blue LEDs. *Agronomy*, 12(10), 2450. <https://doi.org/10.3390/agronomy12102450>
- Zhang, S., Dai, J. & Ge, Q. (2020) Responses of autumn phenology to climate change and the correlations of plant hormone regulation. *Scientific Reports*, 10, 9039. <https://doi.org/10.1038/s41598-020-65704-8>
- Zhang, T., Zhang, Y.H., Yang, J.X., Wang, X.Z., Yang, Q.Q., Zhu, X.J. & Cao, X.Y. (2022a) Transcriptome and targeted metabolome analysis revealed the effects of combined red and blue light on the growth and secondary metabolism of *Scutellaria baicalensis* Georgi. *Industrial Crops and Products*, 188, 115598. <https://doi.org/10.1016/j.indcrop.2022.115598>
- Zhen, S. & van Iersel, M.W. (2017) Far-red light is needed for efficient photochemistry and photosynthesis. *Journal of Plant Physiology*, 209, 115–122. <https://doi.org/10.1016/j.jplph.2016.12.004>
- Zheng, L., Zhang, Q., Zheng, K., Zhao, S., Wang, P., Cheng, J., Zhang, X. & Chen, X. (2020) Effects of diffuse light on microclimate of solar greenhouse, and photosynthesis and yield of greenhouse-grown tomatoes. *HortScience*, 55(10), 1605–1613. <https://doi.org/10.21273/HORTSCI15241-20>
- Zheng, Q., Teo, H. C. & Koh, L.P. (2021) Artificial light at night advances spring phenology in the United States. *Remote Sensing*, 13(3), 399. <https://doi.org/10.3390/rs13030399>
- Zhou, L., Yang, Y. & Feng, H. (2023) Colored plastic film mulching regulates light quality and sucrose metabolism in wine grape in an arid desert oasis. *Journal of Plant Growth Regulation*, 1–10. <https://doi.org/10.1007/s00344-023-11043-7>
- Zhu, X.G., Long, S.P. & Ort, D.R., (2008) What is the maximum efficiency with which photosynthesis can convert solar energy into biomass? *Current Opinion in Biotechnology*, 19, 153–159. <https://doi.org/10.1016/j.copbio.2008.02.004>
- Zoratti, L., Jaakola, L., Häggman, H. & Giongo, L. (2015) Modification of sunlight radiation through colored photo-selective nets affects anthocyanin profile in *Vaccinium* spp. berries. *PLoS ONE*, 10(8), e0135935. <https://doi.org/10.1371/journal.pone.0135935>

How to cite this article: Lauria, G., Ceccanti, C., Lo Piccolo, E., El Horri, H., Guidi, L., Lawson, T. et al. (2024) “Metabolight”: how light spectra shape plant growth, development and metabolism. *Physiologia Plantarum*, 176(6), e14587. Available from: <https://doi.org/10.1111/ppl.14587>