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Review article

Beyond red and blue: Unveiling the hidden action of green wavelengths on plant physiology, metabolisms and gene regulation in horticultural crops

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ABSTRACT

Light intensity, photoperiod and spectral composition drive many fundamental functions of plant life and interacts with other environmental parameters and cultivation factors in determining the crop performance. Indeed, in addition to providing energy to power photosynthesis, light imparts precise signals regulating plant growth, development, and metabolism in photomorphogenesis, through the different wavelengths, detected by specific photoreceptors also at very low fluence rate.

While the efficiency of blue and red wavelengths in the photosynthetic process and their role in photomorphogenesis, as well as their absorption spectra, have been long since demonstrated, green radiation was considered useless (if not even detrimental) for plants for a long time, because of the poor action spectrum of photosynthesis and the weak absorption and high reflection in plant tissues. It is known now that instead the green light sustains photosynthesis in the deeper leaf lamina and canopy layers and participate to several photomorphogenetic processes. However, its role in the complex scenario of plant responses to light environment is still unclear and results in literature are sometimes conflicting.

The aim of this review is to update the knowledge on the effects of green, as both monochromatic light and portion of multispectral radiation, on plant physiology, metabolism, and transcriptional regulation to the most recent advances, with a special focus on those underlying useful agronomic outputs in terms of plant growth and yield, and product quality in vegetable and herbaceous crops. Last findings on these aspects are summarised in order to determine if and how green light-mediated responses can contribute to boost the plant performance in greenhouse and controlled environment horticulture.

1. Introduction

Light quantity, in terms of intensity and duration, and light quality, as spectral composition, influence the plant performance in the whole life cycle, as plants use light as both energy source for photosynthesis (assimilative function) and signal to control many other essential

Abbreviations: ABA;, Abscisic acid; AREB;, ABA-responsive element-binding proteins; ATPase;, adenosine 5′-TriPhosphatase; B;, blue; BES1;, BR transcription factor BRI1-EMS-SUPPRESSOR; BR;, brassinosteroid; BZIP;, basic leucine zipper; Chl;, chlorophyll; CL;, cool light; CRYs;, Criptochromes; CWF;, cool white florescent; DLI;, daily light integral; CRY-DASH;, Drosophila, Arabidopsis, Synechocystis, Homo-Cryptochromes; DEGs;, differentially expressed genes; DW;, dry weight; ETR;, electron transport rate; FAD;, flavin adenine dinucleotide; FL;, fluorescence lamp; FR;, far red; FW;, fresh weight; G;, green; GF;, green florescent; Gs;, stomatal conductance; GS;, glutamine synthetase; GOGAT;, glutamate synthase; HFR1/SICS1;, Long Hypocotyl in Far Red 1/Slender in Canopy Shade 1; HL;, high light; HY5;, Elongated Hypocotyl 5; H_2O_2;, hydrogen peroxide; HPS;, high pressure sodium; LA;, Leaf area; LAI;, leaf area index; LEDs;, Light emitting diodes; LHC;, Light-harvesting complex; LL;, low light; LOV;, Light Oxygen or Voltage; MDA;, malondialdehyde; MH;, metal halide; NI;, night interruption; NR;, nitrate reductase; NiR;, nitrite reductase; NP;, net photosynthesis; NPQ;, non-photochemical quenching; PAR;, Photosynthetically Active Radiation; PCA;, principal component analysis; PIF3;, Phytochrome Interacting Factor3; PHOTs;, phototropins; PHYs;, phytochromes; POX;, peroxidase; PPFD;, Photosynthetic photon flux density; PPE;, phytochrome photoequilibrium; PSI;, Photosystem I; PSII;, Photosystem II; QYinc;, quantum yield on incident light basis; R;, red; SAS;, Shade Avoidance Syndrome; S/R;, shoot/root ratio; SLA;, specific leaf area; UVR8;, UV resistance Locus 8; VOCs;, volatile organic compounds; WL;, white light; WF;, white fluorescent; Y;, yellow; ZTL/FKF1/LKP2;, Zeitlupe/Flavinbinding Kelch Repeat, F-BOX1/LOV Kelch Protein2.

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processes of growth, development and metabolism, in photomorphogenesis (control function) (Devlin et al., 2007). Indeed, besides the photosynthetic pigments (chlorophylls and carotenoids), harvesting light within the range of photosynthetically active radiation (PAR), and other pigments (e.g., anthocyanins), absorbing light without participating to assimilation (hence reducing the light use efficiency in relation to the light absorption), plants evolved sophisticated machineries to perceive and react to light quantity and quality, including highly specific photoreceptors sensing light also beyond the visible spectrum (Weller and Kendrick, 2008). These are classified in four families: phytochromes (PHYs), absorbing red (R, 620–700), far red (FR, 700–775 nm) wavelengths, cryptochromes (CRYs) and phototropins (PHOTs), sensing violet (V, 380–445 nm), blue (B, 445–500 nm) and green (G, 500–580 nm), and Zeitlupe/Flavinbinding Kelch Repeat, F-BOX1/LOV Kelch Protein2 (ZTL/FKF1/LKP2), perceiving blue (Fig. 1). Besides the visible light, ultraviolet (UV) radiation is divided into UV-A (315–380 nm) and UV-B (280–315 nm), with the UV-A further divided into two regions, based on the photoreceptors involved in their detection: the long-wavelength UV-A1 radiation (350–380 nm) requires CRYs and PHOTs, as it is close to B, while the short-wavelength UV-A2 radiation (315–350 nm) requires the UVR8, also sensitive to UV-B (Rai et al., 2020). When exposed to light stimuli, these photoreceptors activate a network of photomorphogenetic pathways, regulating several fundamental functions, including seed germination, seedling establishment, leaf expansion and flowering (Ouzounis et al., 2015).

In general, each light wavelength affects several processes, and each process is regulated by several wavelengths. The R and B promote the stomatal opening, the electron transport, and the Rubisco activity in the photosynthetic process (Zeiger and Zhu, 1998), FR interacts with R, leading to changes in plant architecture and trigging the reproductive process (Zheng et al., 2019a), and it is now known that G sustains photosynthesis in the deepest chloroplasts and the inner leaf layers, and participates to several photomorphogenetic responses (Folta and Maruhnich, 2007). Several wavelengths, including B and UV, stimulate the biosynthesis of antioxidants (i.e., polyphenols, ascorbic acid, carotenoids, and anthocyanins), which enable plants to react to biotic and abiotic stresses, are recognized as healthy compounds for humans, and affect the leaf and flower colour (Andre et al., 2010; Hasan et al., 2017; Samuolienė et al., 2017). At moderate levels, UV-A stimulates photoprotective responses, including the production of stress-protective pigments, antioxidants, and structural changes, enhancing photosynthesis, while at high levels, it can determine oxidative damage and growth inhibition. The UV-B can act as both a signal, activating the biosynthesis of flavonoid and phenolic compounds, and as an oxidative stressor, inducing damage to DNA and Photosystem II (PSII), degradation of chlorophyll and carotenoids, and ROS production, resulting in reduced biomass accumulation.

Hence, photosynthetically inefficient wavelengths are valuable in revealing to the plant important information about the surrounding environment. Accordingly, some photosensitive responses are related to the plant interaction within the ecosystem: for instance, low R:FR ratios are perceived as the presence of other vegetation and activate mechanisms for light competition (*Neighbor detection* and *Shade avoidance Syndrome* - SAS), such as the increase of plant height and shoot/root ratio and the reduction of branching.

Variable light conditions within plant canopies are detected by receptors such as CRYs, PHOTs, PHYs and UVR8, which regulate avoidance responses to limit exposure to excessive or insufficient light, as well as acclimation for unavoidable conditions. In shaded environments, low R/FR ratios suppress PHY B activity, activating PIF factors that promote auxin synthesis and shade-avoidance. This response also relies on COP1, targeted by CRYs, PHYs, and UVR8 (Casal, 2013). Consistently, the light environment has a relevant impact on the plant architecture and on the survival performance.

On these bases, artificial lighting in horticulture can be applied for several purposes: in greenhouse cultivation, to integrate natural light intensity (assimilation light) or to extend the natural day length (photoperiodic light), and in growth chamber for research and *in-vitro* culture and in vertical farms, to totally replace the solar radiation. Due to the complex effects of fluence rate, photoperiod, and spectrum on plant performance, providing the optimal light environment, calibrating efficiently all the light parameters, is one of the major technical challenges to develop successful production systems in protected cultivation (Paradiso and Proietti, 2021) and, even more, in controlled environment agriculture (CEA) (Neo et al., 2022). Specifically, in vertical farming, which implies highly innovative technologies, artificial lighting is the most critical and expensive (Orsini, 2020).

In the past 20 years, a huge progress in lighting technology has been achieved thanks to the light-emitting diodes (LEDs) (Cocetta et al., 2017). Compared to traditional lamps for horticultural application, LEDs allow to tailor the light intensity and spectrum depending on the specific crop requirements, are highly efficient in terms of power conversion, long-lasting, and suitable for different spatial arrangements (i.e., inter-lighting and intra-canopy lighting), optimizing the plant light use efficiency (Bantis et al., 2018).

Light intensity can be a limiting factor in greenhouse, where sunlight decreases compared to outside of a different amount, depending on the structure and the optical features of the cover material (e.g., plastics or

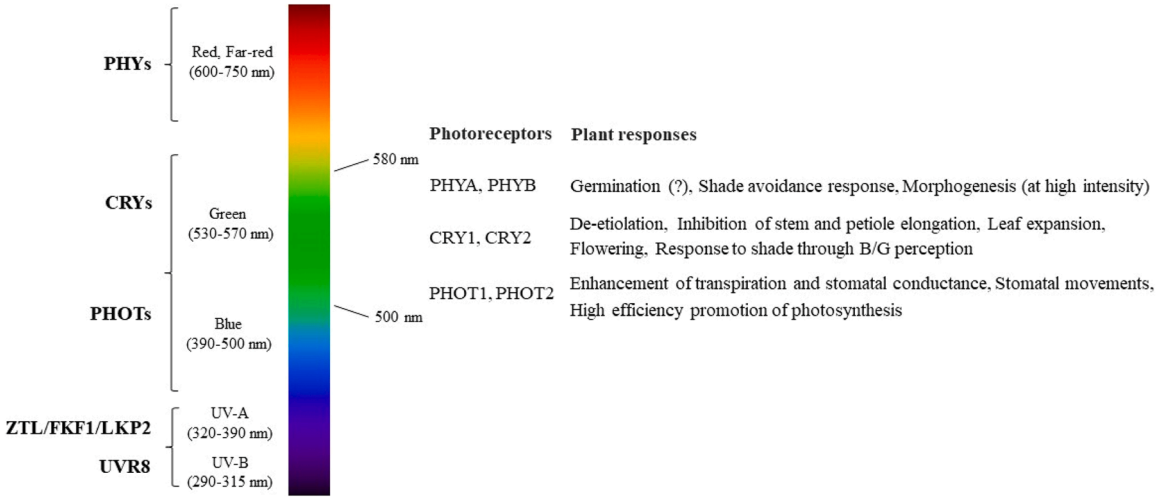

Fig. 1. Spectral wavelength-specificity of the main plant photoreceptors of green wavelengths and related plant photomorphogenetic responses. Phytochromes (PHYs), cryptochromes (CRYs), phototropins (PHOTs), Zeitlupe family proteins (ZTL/FKF1/LKP2), and UV resistance Locus 8 (UVR8).

glass), particularly when solar radiation is limited or unstable (e.g., winter season in Northern countries). Accordingly, in the last years, LED lighting in greenhouse horticulture mainly aimed at assimilation purposes, to increase biomass accumulation and crop yield, with monochromatic R and B diodes in different proportions the most used (Paradiso and Proietti, 2021). However, some of these applications had positive side effects on the nutrient and functional value of several vegetable products (Olle and Viršile, 2013; Bian et al., 2015). At a lesser degree, R and FR are applied in photoperiodic lighting to extend the duration of day or to interrupt the night, to promote flower induction in long day ornamental species, by influencing the phytochrome photo-equilibrium (PPE) (Craig and Runkle, 2016; Proietti et al., 2022). Besides, recent advances in postharvest management of fruits and vegetables gave promising results on the use of R and B LED light as a nonchemical and sustainable technique to preserve the product quality, by controlling the ripening and senescence rate, while stimulating the synthesis of beneficial bioactive compounds and preventing the occurrence of diseases (Ngcobo and Bertling, 2023).

Recent studies have shown that monochromatic or combined LED light can stimulate the biosynthesis and accumulation of substances with high antioxidant activity. For instance, different combinations of R, B, and UV enhance colour development and promote lycopene production in tomato. Some studies have also demonstrated a direct effect on the modulation of genes involved in the biosynthesis of ethylene-related enzymes, such as ACC oxidase (ACO1) and ACC synthase (ACS3). This could have important implications for controlling senescence, particularly in postharvest management (Hasan et al., 2017).

2. Green light: false beliefs and first denials

Green light accounts for a considerable portion of solar radiation. Nonetheless, it has been considered useless for plant life for a long time, based on the weak absorption and high reflection (causing the green appearance of leaves and other plant tissues) and the poor action spectrum of photosynthesis (McCree, 1972). However, contexts where plants experience a green enriched light abound in nature and, as asserted by Folta and Maruhnich (2007), it would be naïve to think that nature did not capitalize light information and stimuli to best adapt to these environments. As a matter of fact, G wavelengths are effectively transmitted within the plant tissues (Massa et al., 2015), and this does suggest a certain role, at least in signalling, in those contexts where plants are not directly exposed to sunlight (Sun et al., 1998). For instance, short plants in the understory develop under a reduced light intensity and an altered spectrum compared to sunlight, with a higher proportion of G and FR, because of the depletion of R and B, massively absorbed by the above vegetation (Vogelmann, 2008). Similarly, in plants with upright *habitus*, while leaves in the higher and external parts of the canopy are exposed to a more direct radiation with higher intensity and broader spectrum, those in the lower and inner parts, receive light transmitted through the mesophyll (self-transmitted) and reflected from the surrounding (leaf-reflected), enriched in green and far red (Fig. 2). In addition, the impact of green light changes in the plant life cycle and

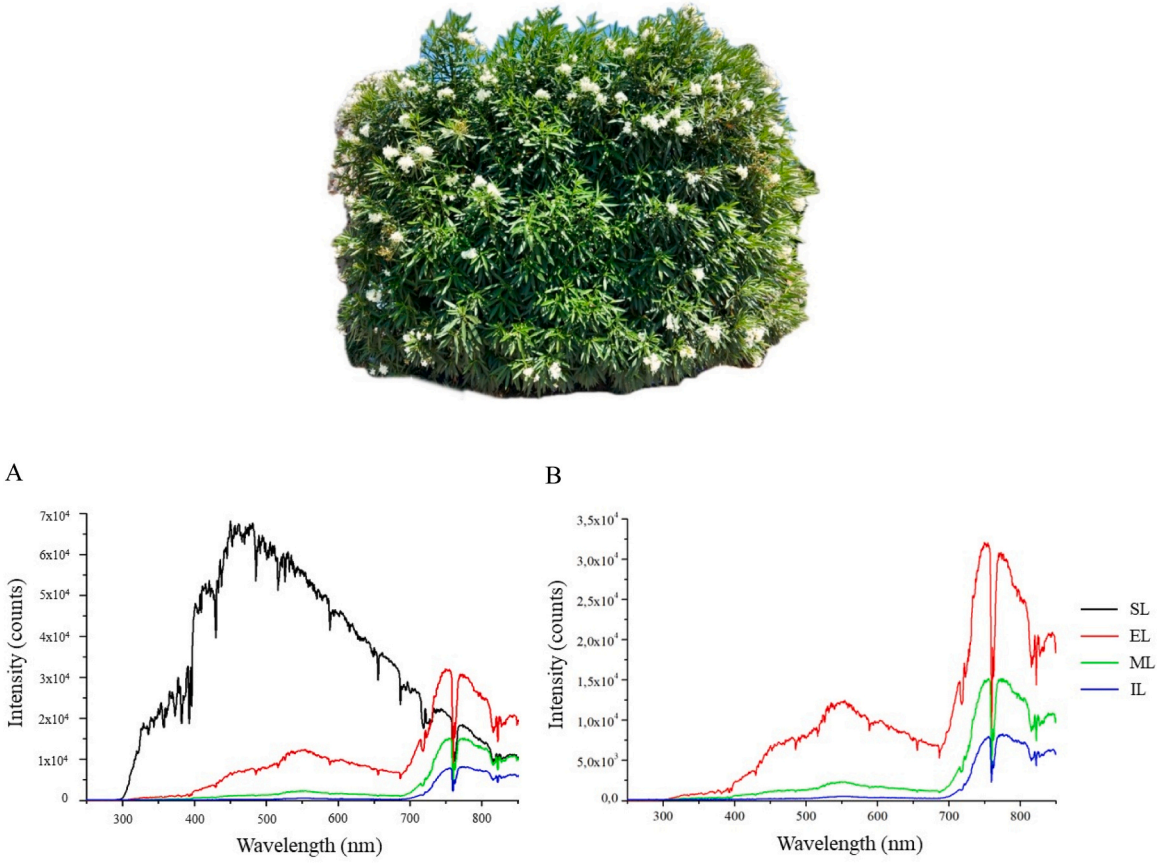

Fig. 2. A) Variations of quantum energy distribution in the range of 250–850 nm in different positions of the canopy in a plant with brush *habitus* (i.e., *Nerium oleander*) compared to full sunlight (SL): a) most external leaves exposed to direct solar radiation (EL); b) middle depth leaves, 30 cm approximately from the external canopy surface (ML); c) inner shaded leaves, 60 cm approximately from the external canopy surface (IL). B) Detail of measurements within the canopy (the range of Y axis was reduced to a half to highlight the variations of the curves in the different wavebands). Measurements were carried out at 12.00 AM, on a sunny summer day (July 16, 2024), in Naples (Italy; 40°51′ N, 14°14′ E), using a spectrophotometer MAYA 2000 pro, equipped with optical fiber with a core of 500 microns and a Software OceanView 2.0 (Ocean Insight, Oxford, UK) (n = 4 per position in the canopy). Radiation intensity is expressed in the arbitrary units calculated by the instrument software.

seems to be crucial in some developmental phases: for instance, during the emergence, etiolated seedlings evolving across the dark soil to the sunny surface have a little chlorophyll content to trap blue and red, hence green exhibits a comparable penetration capacity (Wang and Folta, 2013).

Despite this logic, many pioneer studies in the last century concluded that green radiation had inhibitory effects on plant growth, since the action of G counterposed those of R and B and it mitigated or reversed some promoting effects of B, such as on the stomatal opening and on SAS reactions (including stem elongation and leaf expansion) (Went, 1957; Klein et al., 1965). However, the uselessness or adverse influence of G light was confuted later and a significant role in plant growth and development was theorized then brilliantly demonstrated in the '90s (Klein, 1992). For instance, early simple yet effective experiments showed that plant grew better under a complete white spectrum or when G light was added to B and R background, even though results did not allow to clarify to which extent the positive influence of G arose from a contribution to assimilation or a promotion of certain photomorphogenetic responses. Later, focused measurements revealed that G wavelengths penetrate deeper than R and B in the leaf mesophyll, as well as in the plant canopy, and are absorbed by photosynthetic pigments, hence they promote photosynthesis in the deeper chloroplasts and the lower and inner leaves, increasing the whole-canopy light interception and the assimilation and biomass production (Klein, 1992; Sun et al., 1998; Nishio, 2000). Hence, while R and B are mostly absorbed in the palisade tissue at the adaxial leaf surface, G seeps deeper in the mesophyll and reaches the inner lamina layers, hence adding high intensity G to white spectrum increases the photosynthetic rate (Terashima et al., 2009). Consistently, upscaling photosynthesis data from single leaves to the whole crop through mathematical models revealed a higher utilization of green radiation at the canopy level in rose grown in glasshouse (Paradiso et al., 2011), due to the progressive absorption by internal leaves after repeated reflection within the leaf layers and by the surrounding vegetation, resulting in higher overall photosynthetic efficiency (Fig. 3). Besides, interacting with B, green light influences stomatal opening and controls plant shaping (Klein, 1992). On these bases, it is conceivable that the influence of G had been often undervalued previously because of the insufficient levels applied in the experiments.

In accordance with the above-described evidence, it is known now that green can drive both the short-term response and the long-term acclimation to light environment, through tiny to great adjustments in plant growth and development, acting from the chloroplast- to the whole plant-scale. Consistently with the hypothesis that it mediates plant adaptation within a surrounding vegetation, the reaction to green radiation involves some typical low-light responses of *Neighbour detection* (Ghorbel et al., 2023), implying a decrease in the red and blue fluence rate and changes in the red/far red and red/blue ratios, also leading to changes in the hormonal balance (Brini et al., 2022). Accordingly, it is ascertained that green, alone or combined with other wavelengths, controls a series of physiological, morphological and metabolic responses and that, even though its effects can counter those driven by red and blue, their coaction represents a sophisticated mechanism to finely tune the plant interaction with light environment (Wang and Folta, 2013). Nowadays, a sensory system to detect and respond to green light, combining cryptochrome-dependent and cryptochrome-independent processes and acting in orchestration (rather than in opposition) to red and blue, has been described, and the interaction of green with far red in eliciting some phytochrome-mediated responses has been demonstrated (Smith et al., 2017). Nonetheless, the opinions on the role of G light are currently debated.

Enlightened scientists denied the irrelevance of green light and proved the role of this minor wavelength in the modulation of plant functions with the surrounding light and vegetal environment, and its importance in the light-driven mechanisms underlying the adaptative responses. Valuable review works examined over time the scientific

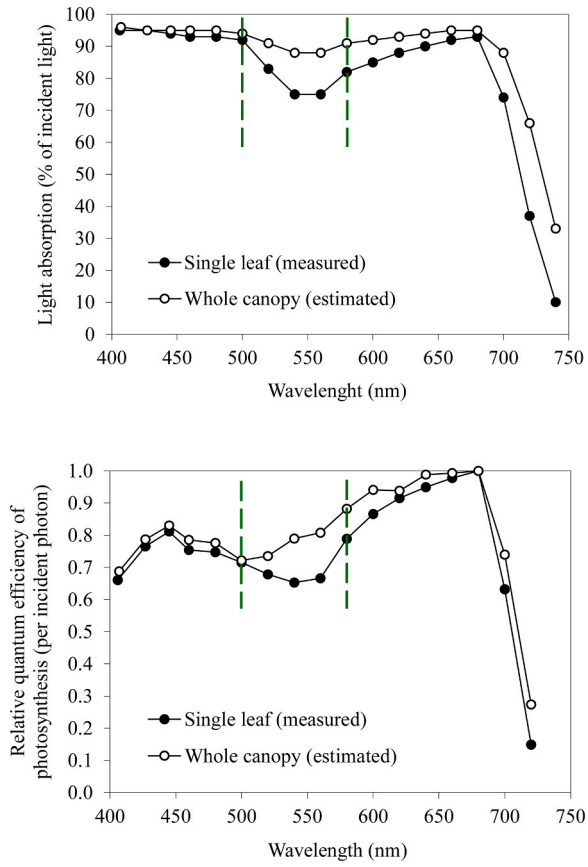

Fig. 3. Light absorption as a percentage of the incident light and Relative spectral quantum efficiency of photosynthesis measured at the single leaf level and simulated at whole canopy level (rose plants for cut flowers grown in glasshouse in Wageningen, The Netherlands, 51°97' N 5°67' E). Re-elaborated from Paradiso et al., (2011).

literature on physiological, metabolic, and genetic plant responses to green as both monochromatic light and portion of multispectral radiation. The aim of this review is to update the knowledge on these aspects to the most recent progress, with a special focus on those determining outputs in terms of plant yield and product quality, in horticultural and herbaceous crops grown in greenhouse and indoor environment. The last findings in plant physiology, metabolisms and gene regulation are summarised to determine if and how green light-mediated responses can contribute to improve the plant performance in protected cultivation and controlled environment horticulture.

3. Method applied for the literature review

The study of scientific literature was performed in Scopus and Google Scholar science databases. With the exception of milestone works reporting pioneer studies or intuitions on light spectrum (e.g., McCree, 1972; Inada, 1976), the literature review referred to the period January 1990-May 2024, however most the articles concentrated after 2000, thanks to the spreading of LEDs. The following keywords were used: green light, green wavelength, green LED, light spectrum, controlled environment, greenhouse, growth chamber, vertical farm. Papers concerning experiments on microgreens and baby leaves, and post-harvest lighting treatments were not considered. A number of 34 review articles and 67 research articles were collected in total, including 3 not concerning higher plants, mentioned in the manuscript about specific topics. Research articles concerned 11 experiments in greenhouse and 54 papers in controlled environment (growth chamber and vertical farm). In terms of crops, 38 articles concerned leafy vegetables, 9 fruit

vegetables, and 12 seed and root crops (Tables 1 and 2). Besides, 13 articles were about *Arabidopsis thaliana* as a model species and 9 about ornamental crops.

The 67 research articles were classified based on the main topics, into four groups: Product Quality (21 papers), Crop Productivity (28 papers), Plant Physiology & Metabolism (52 papers), and Transcriptional Regulation (10 papers). A Venn diagram representing this classification is reported in Fig. 4.

4. Green light and plant physiology and metabolism

In a fascinating and pioneering study performed in the late 1950s, Fritz Went conducted a 6-day experiment on tomato using coloured filters under white fluorescent light to evaluate the effect of G wavelengths. He found that the broad white spectrum, containing a high fraction of G, was less effective in promoting plant growth compared to R and B only (Went, 1957). The results confirmed that chlorophyll (Chl) minimally absorbs G light, supporting the theory assumed for over 60 years that G wavelength is not efficiently utilized in the assimilation process. We are all familiar with the absorption spectra of Chl *a* and Chl *b* which explain the importance of R and B in driving photosynthesis and the marginal impact of G. This is why plant physiologists and producers preferably choose R and B to study photosynthetic regulation, enhance assimilation performance, and promote plant growth. Certainly, Chl *a* and *b*, and carotenoids have a key role in the light-harvesting complexes of photosystems PSI and PSII for linear electron transport. However, the list of photosynthetic pigments now includes new putative green-light-absorbing components such as rhodopsins and heliochrome, which efficiently channel excitation energy to chlorophylls in some species (Folta and Maruhnich, 2007; Golovatskaya and Karnachuk, 2015). Furthermore, chloroplasts reflect 10–50 % of the incident G wavelengths, while the remainder is absorbed or transmitted to deeper leaf layers and lower canopy levels (Nishio, 2000; Terashima et al., 2009).

4.1. Contribution to photosynthesis

Already in the 70 s, some authors demonstrated, in different plant species, that green leaves absorb a substantial fraction of G light (McCree, 1972, Inada, 1976). Differences in the absorption of G wavelengths can lead to variations in the quantum yield efficiency, as demonstrated by McCree as early as 1972, in single leaves and whole-plant canopy, where the photosynthetic quantum efficiency of G was 0.87 μmol electrons μmol^{-1}photons, comparable to R (0.90) and higher than B (0.70) on an absorbed quantum basis.

The differential absorption of R, B and G light within the leaf profile was demonstrated elegantly by studying the profile of internal 14C-fixation within leaf paradermal sections (i.e., slices parallel to the epidermis) in leaves shortly fed with $14CO_2$ and irradiated with G light (Nishio et al., 1993). Sun et al. (1998) showed that in spinach irradiated with R or B at the adaxial leaf side, the carbon fixation was substantially limited to cell layers near the upper leaf surface, while the irradiation with G shifted the distribution of fixed carbon to the inner tissue. Vogelmann and Han (2000) determined the fluorescence profile of spinach leaves irradiated at the adaxial compared to the abaxial side with flashes of monochromatic B, R, and G light (2000 μmol m^{-2} s^{-1}), with peaks at the depths of 50, 100, and 150 μm, respectively, beneath the irradiated surface. Photon transmission through the leaf vertical profile can be compared to the to the passage of particles through a sieve, where Chl *a* and *b*, absorbing mostly in the B and R regions, act as a tight mesh, capturing most of these wavelengths (Smith et al., 2017). In contrast, Chls absorb G light less efficiently, and it is estimated that up to 80 % can pass through the chloroplasts, effectively widening the mesh of the sieve for green photons. Terashima et al. (2009) referred to this effect as the 'green window' of the leaf that, together with the 'detour effect', consisting of the scattering of G light inside the leaf vertical profile (Vogelmann and Han, 2000), increases the possibility to balance the photons absorption by chloroplasts, resulting in higher quantum yield and CO_2 assimilation of G compared to R or B wavelengths (Fig. 5).

The different PAR wavelengths are absorbed by the photosynthetic system with varying efficiency. The energy of each photon is inversely related to its wavelength, meaning, for instance, that the energy content of 1 μmol photons at 400 nm is 0.30 J and 0.17 J at 700 nm (Kume et al., 2016). Therefore, B photons (having shorter wavelengths and higher frequency) offer more energy than R photons. According to the Planck-Einstein relation ($E = hc/\lambda$), where E is the photon's energy (in J), h is the Planck constant (6.626×10^{-34} J·s), c is the speed of light, and λ is the wavelength (nm), B light at 450 nm has an energy of 266 kJ per mol of photons, while R light at 660 nm has 181 kJ per mol, hence B carries about 53 % more energy than R. However, photosynthesis cannot utilize or store the energy surplus from B photons, hence the electron transport per unit of absorbed energy is lower at shorter wavelengths and photosynthesis captures the same amount of energy from both B and R photons (Landi et al., 2020). The authors also highlighted that the average energy value per mol of photons within the PAR 205 kJ mol^{-1}) exceeds the energy requirement for driving the reaction of PSII and PSI (176 kJ mol^{-1} and 171 kJ mol^{-1} respectively), hence the excess is dissipated as heat. Comparing the energy of B and G fractions, B wavelengths (energy value of 270 kJ mol^{-1} at 440–460 nm) produce a higher energy loss than G wavelengths (energy value of 217 kJ mol^{-1} at 540–560 nm), confirming that G light can drive photosynthesis with a quantum efficiency greater than B and similar to R.

Green sustains photosynthesis efficiently even at the whole plant level, reaching chloroplasts of deeper leaves in the canopy. The ability to detect green light can confer a significant advantage to plants in specific environments, such as dense canopies, where green light prevails due to the filtering of other wavelengths by upper leaf layers (Battle et al., 2020). In a dense canopy, lower leaves efficiently absorb and use transmitted and reflected G light thanks to a higher biosynthesis of Chl *b*, absorbing effectively green radiation due to its chemical structure (a CHO group on a side chain of ring II instead of the CH_3 group as in Chl *a*) (Murchie and Horton, 1998; Sun et al., 1998; Nishio, 2000). This metabolic adaptation represents a process of photo-acclimation to shade, where lower leaves adjust their performance to the reduced light conditions (Murchie and Horton, 1998), suggesting that G light acts as a signal for shade avoidance, and it can play a role in fine-tuning photosynthetic efficiency under fluctuating light conditions.

As mentioned, the G light interception by lower leaves in the canopy can allow more equal assimilation along the plant profile. Paradiso et al. (2011) developed a model of the action spectrum at the crop level based on the spectral dependence of photosynthesis at single leaf level in glasshouse rose. Results showed that both light intensity and spectral composition vary and differently influence photosynthesis within the canopy: upper and external leaves received more direct light, with a higher intensity and a broader spectrum rich in R and B, and a significant portion of the scattered G is intercepted by lower and internal leaves, making its absorption at the whole canopy level comparable to that of R light. However, the study on the photosynthetic response of rose leaves lighted at the two leaf sides confirmed that light utilization is more efficient by lighting the adaxial compared to the abaxial side (Paradiso et al., 2020). In rose plants, light absorption and photosynthesis changed under B, G and R wavelengths and in the whole canopy compared to the single leaves (Paradiso et al., 2011). In reddish leaves, the action spectrum of G was 60 % at the leaf level and 68 % at the entire canopy level compared to that of R, while in green leaves, this difference increased and the action spectrum of G was 67 % in single leaves and 78 % in the whole canopy of that of R.

Different published works showed the importance of the interactive effect between light quality and intensity in determining the quantum yield of CO_2 assimilation on an incident light basis (QYinc) (Sun et al., 1998; Evans and Vogelmann, 2003). Terashima et al. (2009) performed an elegant experiment measuring the differential QYinc (in terms of leaf

Table 1
Effects of green light (G, 500–580 nm) added to different background spectra on plant growth, photosynthesis and secondary metabolites content in leafy vegetables.

Species	Cultivar	Lighting conditions: (PPFD = μmol m^{-2} s^{-1}; DLI; daylength) growth environment, lighting treatments		Effects on plant growth, photosynthesis, secondary metabolites		Reference
				Increase	Decrease	
Lactuca sativa L.	Waldmann's Green	PPFD = 150 18 h Growth chamber	RB=B:G:R:FR 24:0:126:2 RGB=B:G:R:FR 23:36:92:2 GF=B:G:R:FR 15:129:6:2 CWF=B:G:R:FR 29:76:45:7	RGB: Leaf area, Fresh Mass, Dry Mass GF: Specific leaf area	CWF: Stomatal conductance (after 24 h exposure)	Kim et al. (2003)
	Waldmann's Green	PPFD = 136; 18 h Growth chamber	RB=B:G:R 21:1:114 RGB= B:G:R 24:6:106	Photosynthetic capacity; Carboxylation efficiency; Leaf number, length and area; Specific leaf area; Shoot FW and DW; total Chl, and Chl a/b ratio: not significantly different between RB and RGB		Kim et al. (2004)
	Red fire	PPFD = 300 12 h Growth chamber	WFL vs BFL = B:G:R 75:24:1 RFL = B:G:R 2:19:79 BFL+RFL = B:G:R 26:22:52	BFL: leaf length/width ratio BFL and BFL+RFL: ascorbic acid RFL: leaf number, SLA, LA RFL and BFL+RFL: total chl	BFL: total carotenoids, soluble sugars, nitrate RFL and BFL+RFL: chl a/b ratio, SLA, shoot DW	Ohashi-Kaneko et al. (2007)
	Outredgeous	PPFD = 300 18 h Growth chamber	FL vs LED R 300 LED R:FR 300 + 20 FL vs LED B:G:R 25 + 5 + 270 LED B:R 30 + 270	R:FR: total biomass, LA, leaf elongation, plant DW B addition: leaf expansion and unrolling BR: anthocyanins	R: plant DW	Stutte et al. (2009)
	Red Fire	PPFD = 100, 200, 300 24 h Growth chamber	FL vs LED G510 (510 nm), G520 (524 nm), G530 (532 nm)	FL 200: LA and leaf FW, S/R, G at increasing PPFD: root DW G510 300: leaf number, petiole length G520 and G530 100 and G530 300: petiole length G510 and G520 increasing PPFD: petiole width G 200 and G510 100: Pn	FL 300: leaf length and width, S/R G: LA, leaf FW, shoot DW G 200 and 300: S/R FL and G510 increasing PPFD: SLA	Johkan et al. (2012)
	Red Sunmang, Green Grand Rapid TBR	PPFD = 173 12 h Growth chamber	FL vs LED R9B1 = B:G:R 1:0:9 R9G1 = B:G:R 0:1:9 R8B2 = B:G:R 2:0:8 R8G1B1 =B:G:R = 1:1:8 R7B3 = B:G:R 3:0:7 R7G1B2 = B:G:R 2:1:7	R: FW and DW of shoot and root, R and B: LA Increasing B: SLDW (both cvs) R8G1B1 and R7G1B2: shoot FW, chls (Sunmang) R8G1B1: chls (Gran Rapid)	FL and R7B3: plant FW (in Gran Rapid TBR), R9G1: SLDW (both cvs), chls (in Gran Rapid TBR)	Son and Oh (2015)
	Waldmann's Green	PPFD = 200, 500 16 h Growth chamber	Warm, Neutral, Cool white R, G, B, RB, RGB LEDs	B: DM, SLA, SLA 500 PPFD: DM, LAI, NP 500 PPFD and B: DM, NP	G: LAI, Chls 500 PPFD: SLA	Snowden et al. (2016)
	Green Oak Leaf	PPFD = 135 and 105 W LEDs 16 h Growth chamber	W LED vs W LED + FR, R, Y, G, B LEDs (30 PPFD each)	W*R* and WB: shoot FW WFR: S/R ratio, ascorbic acid	WFR: shoot FW, biomass, pigments	Chen et al. (2016)
	Butterhead	PPFD = 200 12 h and preharvest continuous light (CL) Growth chamber	RB-CK= B:G:R 40.1:0:161.7 RB-CL= B:G:R 40.7:0:162.5 RBG-CL= B:G:R 33.6:33.4:134.8 W-CK= B:G:R 83.8:84:33.8 W-CL= B:G:R 84:84.5:33.6	RBG-CL: shoot FW, total DW, DPPH, total phenolics, SOD activity	RBG-CL: Nitrate content, POD activity, MDA content, Chl Fluorescence	Bian et al. (2016)
	Butterhead	PPFD = 200 12 h and preharvest continuous light (CL) Growth chamber	RB-Control= B:G:R 1:0:4 RB-CL= B:G:R 1:0:4 RBG-CL= B:G:R 1:1:4 rb-CL= B:G:R 1:0:1 rbg-CL= 1:1:1	RBG-CL: Pn, DPPH, Ascorbic acid, Soluble sugars, Soluble proteins (24 h); Fv/Fm, Total phenols, DPPH, Soluble sugars, Soluble proteins (48 h) RBG-CL and rbg-CL: Fv/Fm (24 h); Ascorbic Acid (48 h)	RBG-CL and rbg-CL: MDA, Nitrate content (24 h and 48 h)	Bian et al. (2018)
Spinacia oleracea L.	Okame	PPFD = 300 12 h Growth chamber	WFL vs BFL = B:G:R 75:24:1 RFL = B:G:R 2:19:79 BFL+RFL = B:G:R 26:22:52	BFL: total chl, chl a/b ratio, total carotenoids RFL+BFL: ascorbic acid	BFL: shoot DW, LA, leaf length/width ratio, petiole length RFL: soluble sugars, nitrate	Ohashi-Kaneko et al. (2007)
	PD512	PPFD = 190 12 h Growth chamber	R4B1 = B:G:R 1:0:4 R5B2G3 = B:G:R 2:3:5 R1B1G1 = B:G:R 1:1:1	R5B2G3: SLA, Chlb, carotenoids, organic acids content, stomatal width	R1B1G1: FW, DW, NAR, Chlb, carotenoids, leaf compactness,	Nguyen et al. (2021)

(*continued on next page*)

Table 1 (*continued*)

Species	Cultivar	Lighting conditions: (PPFD = μmol m^{-2} s^{-1}; DLI; daylength) growth environment, lighting treatments		Effects on plant growth, photosynthesis, secondary metabolites		Reference
				Increase	Decrease	
					thickness, palisade and spongy tissue	
Brassica campestris L.	Komatsuna	PPFD = 300 12 h Growth chamber	WFL vs BFL = B:G:R 75:24:1 RFL = B:G:R 2:19:79 BFL+RFL = B:G:R 26:22:52	RFL: shoot DW, LA, BFL: SLA, ascorbic acid	RFL+BFL: SLA, leaf length/width ratio, RFL: chl a/b ratio, carotenoids BFL: total chls, soluble sugars RFL and RFL+BFL: ascorbic acid	Ohashi-Kaneko et al. (2007)
	Te'aiqing	PPFD = 150 12 h Growth chamber	LED B, G, Y, R, R:B (6:1)	R: plant height B: soluble sugar, chl a/b RB: soluble protein, chls	R: chls Y: plant DW, soluble sugar, proteins G: chl a/b B, RB: plant height	Fan et al. (2013)
	Improved Genovese Compact, Red Rubin	PPFD = 220 16 h Growth chamber	R76B24 = B:G:R 53:0:169 R44B24G32 = B:G:R 54:70:97 R74B16G10 = B:G:R 36:22:165 R42B13G45 = B:G:R 28:98:93	R44B24G32 and R42B13G45: plant height (both cvs), SLA (RedRubin) R42B13G45: plant width (RedRubin)	R42B13G45 (RedRubin): Pn, E, Gs, SPAD R44B24G32 and R42B13G45 (RedRubin): Shoot FW and DW, phenolics, flavonoids, antioxidant capacity R74B16G10 and R42B13G45 (Genovese): phenolics, flavonoids, antioxidant capacity R42B13G45 (Genovese): anthocyanin	Dou et al. (2019)
	Improved Genovese Compact, Red Rubin	PPFD = 224 16 h Growth chamber	R88B12 = B:G:R 12:0:88 R76B24 = B:G:R 24:0:76 R51B49 = B:G:R 49:0:51 R44B12G44 = B:G:R 12:44:44 R35B24G41 = B:G:R 24:41:35	R44B12G44 (both cvs): plant height	R44B12G44 and R88B12 (Red Rubin): Pn R44B12G44 (Red Rubin): SPAD, LA All treatments with green: fresh and dry weight (both cvs) R44B12G44 and R35B24G41 (both cvs): Phenolics, Flavonoids, Antioxidant capacity	Dou et al. (2020)
Ocinum basilicum L.	Lettuce Leaf, Red Rubin	PPFD = 200 24 h Growth chamber	FL vs LED B:G:R:FR 12:19:61:8 B:G:R:FR 8:2:65:25 B:G:R:FR 14:16:53:17 UV:B:G:R:FR 1:20:39:35:5	FL, G2, G19 in Lettuce Leaf, G2 in Red Rubin: growth rate FL: LA (both cvs) G16 in Lettuce Leaf: root length G2, G16, UV1: total biomass (both cvs) UV1: root/shoot ratio (both cvs) FL, G16 in Lettuce Leaf, G19 in Red Rubin: new roots development UV1: phenolics (both cvs)	FL = root/shoot ratio (both cvs)	Bantis et al. (2016)
	Zhonghuang 3 (ZH3)	PPFD = 100 and 100 + 300 12 h and 12 + 4 Growth chamber	CK= white light 12 h GL= white light 12 h + G 4 h BL= white light 12 h+ B 4 h BG= white light 12 h + BG 4 h	BG: catechins, procyanidins, anthocyanins GL: L-ascorbate, SA	BG: Phenylalanine	Zheng et al. (2019a,b)
	Amara, Red Giant, Siberian, Scarlet	PPFD = 224 16 h Growth chamber	R88B12 = B:G:R 12:0:88 R76B24 = B:G:R 24:0:76 R51B49 = B:G:R 49:0:51 R44B12G44 = B:G:R 12:44:44 R35B24G41 = B:G:R 24:41:35	R44B12G44: SPAD (Scarlet), Plant height (Amara, Siberian, Scarlet), FW (all cvs), DW (Red Giant and Scarlet) R35B24G41: Antioxidant activity, Phenolics (Siberian, Scarlet) R44B12G44 and R35B24G41: Anthocyanins (Siberian)	R44B12G44 and R35B24G41 (Siberian), and R44B12G44 and R35B24G41 (Scarlet): Pn	Dou et al. (2020)
	Tigullio (green), Red Rubin (red)	PPFD = 250 additional to ambient light 5 h Greenhouse	R B G W = B:G:R 1:1:1	Tigullio G: WUEi Red Rubin R: Ch B: Flavonoids	Tigullio R: DM, N° of stomata, Pn G: ETR Red Rubin R: N°of stomata, Flavonoids	Lauria et al. (2023)

CO_2 assimilation) after the addition of monochromatic R and G at varying intensities to a white light background. The PPFD of monochromatic light was either 50 μmol m^{-2} s^{-1} (for white light applied at 0, 40, 100 and 150 μ mol m^{-2} s^{-1}) or 150 μ mol m^{-2} s^{-1} (for white light at 200, 450, 700, 950 and 1.200 μ mol m^{-2} s^{-1}). At low white background intensity, R showed a higher differential QYinc than G, due to the low G absorption, while at high white background the QYinc of the added G decreased slower at increasing light density compared to R, and

Table 2
Effects of green light (G, 500–580 nm) added to different background spectra on plant growth, photosynthesis and secondary metabolites content in fruit vegetables and seed and root crops.

Species	Cultivar	Lighting conditions: (PPFD = μmol m^{-2} s^{-1}; DLI; daylength) growth environment, lighting treatments		Effects on plant growth, photosynthesis parameter, metabolites		References
				Increase	Decrease	
Capsicum annuum L.	California Wonder	PPFD = 200 and 500 16 h Growth chamber	Warm, Neutral, Cool white R, G, B, RB, RGB LEDs	B: NP, Chls 500 PPFD: DM, LAI 500 PPFD and B: NP	B: plant DW, LAI, stem and petiole length G: SLA 500 PPFD and B: DM	Snowden et al. (2016)
Cucumis sativus L.	Sweet Slice	PPFD = 200 and 500 16 h Growth chamber	Warm, Neutral, Cool white R, G, B, RB, RGB LEDs	B: NP, Chls G: LAI 500 PPFD: DM, LAI, NP	B: stem and petiole length, plant DW, LAI, SLA G: NP, chls 500 PPFD and B: DM 200 PPFD and B: NP	Snowden et al. (2016)
Solanum lycopersicum L.	9 genotypes	PPFD = 200 and 500 16 h Growth chamber	Warm, Neutral, Cool white R, G, B, RB, RGB LEDs	B: Chl G: stem length 500 PPFD: DM, LAI 500 PPFD and B: DM, NP	B: plant DW, LAI, stem and petiole length 500 PPFD and B: DM	Snowden et al. (2016)
	Komeett	PPFD = 171 13 h d^{-1} until day 26, then 16 h d^{-1} until day 39 Glasshouse	RB= B:G:R 4.6:1.1:94.4 G_{Low}= B:G:R 4.1:16.4:79.5 G_{High}= B:G:R 3.1:41.1:55.8	Chl a:b ratio, carotenoids, and day respiration increased with G light %	G_{Hight}: Amax (halfway measurement, no differences in following measurements)	Kaiser et al. (2019)
Raphanus sativus L.	Cherry Belle	PPFD = 200 and 500 16 h Growth chamber	Warm, Neutral, Cool white R, G, B, RB, RGB LEDs	B: NP and Chls G: petiole length 500 PPFD: LAI 500 PPFD and B: DM, NP	B: plant DW, stem and petiole length, LAI G: DM	Snowden et al. (2016)
	Zara	PPFD = 100 12 h Growth chamber	L1 = B:G:R:FR 0:0:100:0 L2 = B:G:R:FR 16:0:78:3 L3 = B:G:R:FR 16:0:74:3 + 4UV L4 = B:G:R:FR 32:15:139:6 L5 = B:G:R:FR 16:0:72:3.2 + 5.5 Amber	L3: Total phenols L4: Vitamin C, α-T L5: DPPH	L1: DPPH L4: Total phenols L2: Vitamin C, α-T	Samuoliene et al. (2011)
Triticum aestivum L.	Sirvinta 1	PPFD = 100 12 h Growth chamber	L1 = B:G:R:FR 0:0:100:0 L2 = B:G:R:FR 16:0:78:3 L3 = B:G:R:FR 16:0:74:3 + 4UV L4 = B:G:R:FR 32:15:139:6 L5 = B:G:R:FR 16:0:72:3.2 + 5.5 Amber	L4: DPPH, α-T L3: Total phenols, Vitamin C	L1: DPPH, Vitamin C, α-T L5 Total phenols	Samuoliene et al. (2011)
	Ningchun	PPFD = 500 16 h Growth chamber	Top lighting vs Top + Intra-canopy lighting 70R20B10G= B:G:R 20:10:70 70R10B20G= B:G:R 10:20:70 70R30B= B:G:R 30:0:70 80R10B10G= B:G:R 10:10:80 80R20B= B:G:R 20:0:80 90R10B= B:G:R 10:0:90	All TL+IC treatments (except 70R10B20G): Pn 80R10B10G (RI): Plant height 70R20B10G, 70R10B20G and 80R10B10G (both TL and TL+IC): Tiller number 70R20B10G and 80R10B10G (TL+IC): LAI 70R20B10G, 80R10B10, and 90R10B (TL+IC): Seed yield	All TL+IC treatments shortened the growth cycle	Shen et al., (2020)

eventually overtaken it. In other words, high-intensity white light provides a large amount of excitation energy to chloroplasts located near the leaf adaxial surface, positively regulating non-photochemical quenching (NPQ) and causing dissipation of the energy excess as heat, so under such conditions the additional R light cannot be used efficiently. Conversely, a low excitation energy from the high intensity white light can reach the chloroplast deeper in the mesophyll, so additional green can be used in photosynthesis more efficiently than R. Consequently, the inclusion of green in artificial light in controlled environment stimulates photosynthesis in the deeper leaf and canopy layers, enhancing carbon gain and potentially increasing crop yield (Liu and Van Iersel, 2021).

4.2. Contribution to metabolism

The G light not only contributes distinctively to photosynthesis but also plays an important role in the regulation of metabolic and photomorphogenic processes, facilitating the plant acclimation to short-term environment changes and influencing long-term development, through modulation of stomatal opening, chloroplast gene expression, photoperiodic flower induction, stem growth, and plant shape (Golovatskaya and Karnachuk, 2015). When plants perceive light, approximately 30 % of their transcriptome changes, resulting in complex interactions to efficiently utilize the available radiation (Wu et al., 2014). The mechanisms allowing plants to sense G light have not completely unveiled, but it is clear to date that plant reaction implies responses dependent to cryptochromes (CRYs), to phytochromes (PHYs), or to a putative uncharacterized green-light photoreceptor (cryptochrome-independent pathways) (Bouly et al., 2007).

CRYs absorb UV-A and blue light, through the chromophore flavin adenine dinucleotide (FAD), existing in three redox states, each absorbing photons at different wavelengths (Bouly et al., 2007; Kao et al., 2008). When the oxidized and inactive FAD absorbs UV-A/blue light, it is converted to a neutral radical FADH or an anion FAD^{-}, that

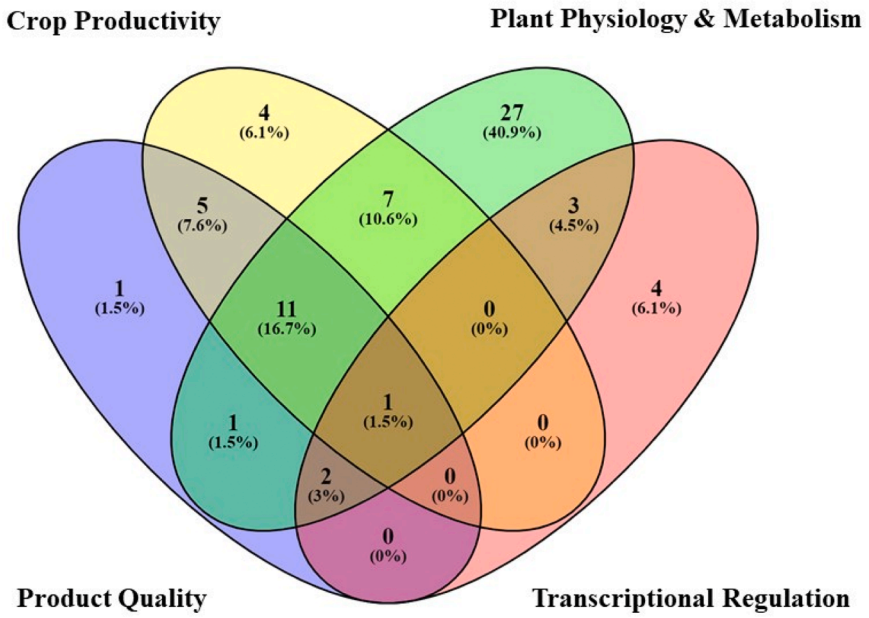

Fig. 4. Venn diagram representing the classification of the 67 research articles collected through the literature review based on the main topics. The distribution in each group is reported as the percentage of the total as well as the number. The diagram was created using Venny 2.1.0 software (Oliveros J.C., 2007–2015; https://bioinfogp.cnb.csic.es/tools/venny/index.html). Four different colours were assigned to the 4 main categories, and papers were grouped depending on whether they belonged to a single category or multiple categories, creating subsets with colours derived from the overlap of the main categories.

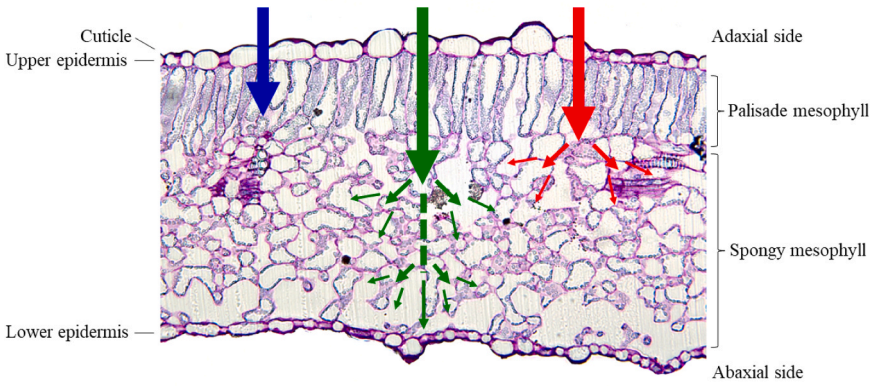

Fig. 5. Depth of penetration of monochromatic blue (B), green (G), and red (R) wavelengths through the leaf profile in leaves lighted from the adaxial surface, according to the models proposed by Vogelmann and Han (2000) and Terashima et al. (2009). The B photons are mainly absorbed in the upper cell layers (palisade parenchyma), the R photons penetrate deeper in the underlying mesophyll, and both are absorbed by the more surface chloroplasts, while G photons are weakly absorbed by chlorophylls and hence transmitted through the chloroplast (up to 80 % of the fluence rate), passing to the spongy mesophyll.

activates the cryptochrome and initiates UV-A/blue-light responses. However, the FAD^{-} anion can also absorb G light, that reduces it to a $FADH^{-}$ or $FADH_2$ form, inactivating the CRYs and reverting these responses (Talbott et al., 2002; Sellaro et al., 2010). Bouly et al. (2007) demonstrated that, *in vivo*, in *Arabidopsis* the *cry1 cry2* activation by B light can be inhibited by G light, consistently with a change of the cofactor redox state. Studies have shown that some B CRYs-mediated responses can be reverted by G, suggesting an antagonistic relationship between G and B wavelength on CRYs activation (Folta and Maruhnich, 2007; Smith et al., 2017). This reversible effect on CRYs responses activation is strictly dependent on the B/G ratio and longer G wavelengths (570 nm) (Battle and Jones, 2020; Thoma et al., 2020). Moreover, some studies report that shorter wavelengths (<530 nm) have a synergistic effect on CRY signalling pathways while longer wavelengths (>530 nm) tend to produce antagonistic effects (Battle and Jones, 2020). The differences between the effects induced by short- and long- green wavelengths suggest that further photoreceptors, and related light-activated pathways, could be involved in the modulation of G light signalling in addition to CRYs and FAD chromophore.

The reversible responses triggered by the B/G ratio are not shown in a CRYs-knockout mutant of *Arabidopsis*, clearly confirming a dependency on CRYs, however other responses to G are present, supporting the hypothesis of the existence of another G-light photoreceptor. Battle and Jones (2020) suggested that, in addition to CRYs, also PHYs absorb a portion of the G waveband, even though with a lower sensitivity than for R wavelengths. Indeed, PHYs preferentially absorb long wavelengths G (530–590 nm) as well as yellow photons (Más et al., 2000). For this reason, yellow light perceived by PHYs could trigger antagonistic responses to those mediated by CRYs, while short wavelengths G (500–530 nm) prolong CRYs signals or initiate low-fluence B responses. Notably, the circadian gene expression shows different roles for CRYs under G and under B lighting, and PHYs could cooperate to

regulate circadian responses to G (Battle and Jones, 2020). In CRY mutants *cry1cry2* seedlings of *Arabidopsis*, B results in low-amplitude rhythms, while G and B together increase the amplitude and extend the circadian free-running period. These results suggest either a distinct contribution of G and B on cryptochrome-mediated rhythmicity, or a synergistic regulation by PHYs and CRYs of the circadian perception of green light (Battle and Jones, 2020).

Longer G wavelengths (540 nm) reverse the B-induced stomatal opening in many monocotyledonous species: in onion (*Allium cepa*) and oat (*Hordeum vulgare*), G-B at ratio 2:1 induced an almost complete reversal of the stomata opening obtained with B alone, while at ratio 1:1 resulted in an intermediate closure (Talbott et al., 2006). Green reversibility of the B-induced opening was also found in dicotyledonous commonly used in research on stomata, as the model species *Arabidopsis thaliana*, pea (*Pisum sativum*), dayflower (*Commelina communis*), and tobacco (*Nicotiana tabacum* and *Nicotiana glauca*) (Jewer et al., 1985; Assmann and Schwartz, 1992): G:B 2:1 produced about 100 % reversal of stomata opening in all cases, while G:B 1:1 about 50 % reversal in *Vicia faba* (Frechilla et al., 2000; Talbott et al., 2006). This evidence suggests that reversibility could be a basic photobiological property of guard cells, rather than the adaptation to specific light environments (Talbott et al., 2006). At the same time, stomata opening suppression can be reduced by the G removal, especially in phototropin mutants, and in the absence of zeaxanthin, suggesting a potential role of this pigment as G-absorbing chromophore (Battle and Jones, 2020).

The G light inhibits the B-induced flowering (Banerjee et al., 2007), reduces B-stimulated anthocyanin biosynthesis (Zhang and Folta, 2012), and can promote seed germination via PhyA (Shinomura et al., 1996), and CRY1 overexpression leads to green light hypersensitivity (Bouly et al., 2007). The absence of cry2 inhibits G-induced accumulation of salicylic and jasmonic acid and suppresses root elongation (Sato et al., 2015). Moreover, G can change gene expression, repressing plastid-encoded transcripts, and maintain circadian rhythms in seedlings independently of CRYs, that regulate the circadian cycle. These findings suggest that G is perceived through multiple interconnected photoreceptors, initiating specific photomorphogenic responses.

The G light perception, particularly in terms of B/G ratio, could be considered as an alternative and fine-tuned signalling mechanism for plant adaptation to shade (Zhang et al., 2011). An increase in the G light portion in a B-R background activates similar responses to those observed in shade avoidance, mediated by PHYs through the R/FR perception (Sellaro et al., 2010; Smith et al., 2017). It is demonstrated the role of PHYs as sensors of R and FR wavelengths and in the perception of R/FR ratio as a shade signal. However, the spectrum reaching the shaded parts of the canopy is also enriched in G wavelengths. Hao et al. (2023) suggested that the brassinosteroid (BR) signalling pathway is involved in the process of G-promoted hypocotyl elongation, by the activation of a key BR transcription factor (BRI1-EMS-SUPPRESSOR - BES1). This pathway mediated by G acts as a shade signalling to enable plants to adapt to a G-light-dominant environment under a canopy and represents an alternative way that does not involve PHYs and CRYs. In this context, the G effect is additive to those of FR, promoting hypocotyl growth, leaf epinasty and petiole elongation, and reducing leaf expansion. In basil (*Ocimum basilicum*), additional G to a white spectrum increased biomass production, stem length, and leaf area, confirming the hypothesis that G induces shade avoidance phenotypes (Schenkels et al., 2020). In this case, the observed stem elongation and leaf expansion suggests that G could be used to improve the appearance and the commercial value of basil (Schenkels et al., 2020). In tomato, the partial replacing of R and B by G increased stem length, stem and leaf biomass, specific leaf area, and carotenoid concentrations in the middle canopy (Kaiser et al., 2019).

Contrary to photoreceptors of R and B, whose roles in plant physiology and metabolism are well understood, the existence of a putative specific photoreceptor for G, triggering response pathways independent to CRYs or PHYs activity, remains unclear. Several candidates have been proposed as potential G light receptors. A specific G photoreceptor was suggested as a regulatory pigment, controlling the germination of *Lolium rigidum* seeds, since B and G interrupt the dormancy regardless of FR. This interruption can be established with G and without the participation of CRY (Golovatskaya and Karnachuk, 2015). In a worthy review, Folta and Maruhnich (2007) provided some suggestions for potential specific G photoreceptors, indicating the carotenoid zeaxanthin, required for the B-G reversible stomatal regulation, as a receptor absorbing both B and G while switching between active and inactive states. Another intriguing candidate is a flavoprotein isolated from *Cucurbita pepo* and *Phycomyces*, although there is no evidence of light effects above 500 nm *in vitro*. CRY3 (or CRY-DASH) is another flavoprotein with high local sequence similarity to CRYs and photolyases, localized in the chloroplast, up-regulated in green light (Dhingra et al., 2006).

5. Green light and transcriptional regulation

The investigation into the regulatory mechanisms triggered by green light in plants has evolved from studies focusing on mechanisms of dark adaptation and shade avoidance. Numerous studies have been conducted on *Arabidopsis thaliana*, a species known for its shade-avoiding characteristics. These response mechanisms are stimulated by shading conditions, which lead to a reduction in the R/FR radiation. A substantial body of research has identified Phytochrome B (PhyB) as the primary regulator of SAS (Wang and Folta, 2013). Downstream of the PhyB-regulated morphological adaptation mechanisms, the action of a negative regulatory gene known as *HFR1/SICS1* plays a crucial role in maintaining a balance in adaptive responses (Sessa et al., 2005; Ruberti et al., 2012). During shading, also the B components of light decrease, and the plants adaptive responses includes the Cryptochrome-mediated action of the hormone ethylene (Wang and Folta, 2013). Several studies conducted on model plants have demonstrated that green light promotes the modulation of ABA production and stomatal opening (Smith et al., 2017). This prior knowledge is now crucial for developing and applying strategies to modulate responses to water stress in agriculturally and nutritionally important crops.

As mentioned, to date a specific photoreceptor for green light has not been identified; however, several studies have demonstrated that green light can elicit certain responses and modifications in various photoreceptors such as PHYs and CRYs (Wang and Folta, 2013; Smith et al., 2017). Downstream of photoreceptor stimulation, activations of specific gene families and transcription factors typically observed can be studied to identify the mechanisms and modes of action through which specific light inputs (including G as monochromatic radiation or as part of more complex spectra) affect plant physiology and metabolism.

First studies conducted primarily on model plants enabled the deciphering of the mechanisms underlying the interaction between green light and plants. Today, these studies serve as the foundation for applied research programs, which are also beneficial in agriculturally relevant crops. Also, advancements in analytical innovation enable the application of particularly effective and precise analytical approaches to the study of economically significant plant species, not just model plants. This opens vast possibilities for innovation in the field of agro-food and ornamental plant production, which are often conducted in controlled environment or indoor cultivation systems and often include the use of modern artificial lighting systems (e.g., LEDs).

A study conducted in 2018 elucidated some of the main effects of green light on the growth of lettuce plants (Bian et al., 2018). It was observed that the addition of green to blue and red light resulted in an overexpression of some key genes regulating the photosynthetic response. The genes investigated were *Psb*A, which encodes for the photosystem II protein D1 and it's related to photodamage and photoinhibition responses, and *LHCb*, belonging to the LHC gene family and encoding several light-harvesting Chl a/b-binding (LHC) proteins. This gene is essential for the control and distribution of excitation energy in

the photosynthetic system. The study consisted in an indoor experiment, employing continuous artificial light over a period of 48 consecutive hours. The authors demonstrated that the genes under consideration exhibited a transient upregulation over time, with a pronounced increase within the initial 12 h following the light treatment, a decrease or stabilization in transcripts between 12 and 24 h, and subsequent downregulation between 24 and 48 h. The data obtained from the gene expression analysis were consistent with a mitigation of oxidative stress resulting from the continuous lighting and a general maintenance of the photosynthetic potential (Bian et al., 2018).

The effects of green light on the photosynthetic apparatus and stomatal closure regulation have also been studied in tomato plants subjected to drought (Bian et al., 2019). In addition to an effect in terms of regulation and modulation of stomatal conductance, the study demonstrated that green light has a repressive effect on the expression of the genes *SlHA1*, *2*, and *4*, which encode for plasma membrane H+ -ATPases enzymes, which are fundamental for stomatal regulation and activation of the signalling pathway linked to the gene *SlAREB1* (ABA-responsive element-binding proteins: AREBs), leading to improved drought tolerance. This study opens new perspectives regarding the potential applications of green light in controlled environment production systems, as it demonstrated that green can be utilized to improve water use efficiency, a fundamental aspect for enhancing the sustainability of indoor productions.

The development and expansion of "omics" or "high-throughput" analytical techniques nowadays allow for an in-depth study of transcriptional responses of agricultural crops to various environmental stimuli, including light. The cost of these analyses is progressively decreasing, enabling their increasing use also in studies focused on cultivated plants. In this context, the advance in investigative techniques, based on RNA extraction, sequencing, and subsequent annotation and expression analysis, enabled in recent years detailed studies focusing on the transcriptome analysis. This approach facilitates the collection and analysis of a vast amount of data concerning the expression of thousands of genes and transcription factors, allowing for the identification of responses to light stimuli (particularly green light), across various crops. To date, the number of published studies that use exclusively green light is still limited, but the application of these techniques has led to the identification of important responses in certain species of interest.

An interesting example is represented by a study conducted on tomato plants grown under optimal and drought conditions, illuminated with monochromatic R, B, and G lights (Bian et al., 2021). The transcriptome analysis allowed to observe a positive effect of G light in mitigating water stress, and to describe the activation mechanisms and the majorly implicated pathways. In addition to the already known role of G light in stomatal regulation, the study highlighted and elucidated the role of ABA and its related metabolic pathways. A total of 3850 differentially expressed genes (DEGs) were identified, and important responses were found in both ABA biosynthesis and transduction. The transcription factor *HY5*, belonging to the bZIP family, appeared to be particularly involved in the green light-mediated response to water stress. Moreover, the transcription factors *WRKY46* and *WRKY81* also seemed to play a key role in ABA accumulation.

An intriguing study published in 2019 compared the effects of B and G light (and their combination) on tea (*Camellia sinensis* L.) plants using an RNAseq-based analysis approach (Zheng et al., 2019b). The study allowed the identification of an important number of genes (1525) that were uniquely stimulated by G light, and not by B light or a combination of G and B. The findings indicated that in some cases, green light partially attenuated the transcriptional responses induced by blue light. Notably, important modulators of light signal coordination, such as *HY5* (as found in tomato) and several *R2R3-MYBs* transcription factors, were significantly repressed in response to green light or induced in response to blue light or the combination of both wavelengths. Green light induced the downregulation of the *PHOT2* gene, involved in growth and developmental modulation processes, and a slight overexpression of the *PIF3* gene, which plays a role in shade avoidance mechanisms.

Among the genes specifically influenced by green light are those primarily implicated in signalling (phosphorylation, ion homeostasis, and transport), developmental processes (cellular macromolecular complex assembly, protein metabolism, secondary cell wall biogenesis, response to ethylene, cytokinin, and auxin), regulation of shade avoidance, control of water loss (response to ABA, osmotic stress), and biotic stress response. One of the most significant conclusions from this study is the necessity to further investigate the application of green light in combination with other wavelengths rather than as a monochromatic light. This is of particular interest, especially in the application of these approaches in commercial production context. Additionally, the study showed a significant activation of metabolic pathways related to defence against both biotic and abiotic stress. In this regard, green light appears to play a role in promoting the synthesis of bioactive nutritionally relevant compounds, such as ascorbic acid and benzoic acid derivatives, which can help in promoting a higher quality of the produce.

6. Green light and plant growth

Pioneer experiments to evaluate the effects of the different wavelengths were carried out using traditional multichromatic light sources, such as high pressure sodium (HPS) or fluorescent (FL) lamps, with different emission spectra (and heat dispersion, adding a parallel effect on temperature), making difficult to discriminate the specific contribution of each one. Besides, these studies reported inconclusive or conflicting results, likely due to methodological problems (e.g., some reports expressed light intensity in improper unit of measurement like foot-candles). Technical problems also occurred in the initial experiments with LEDs: for instance, the first commercial green diodes emitted a little blue or red light. In addition, when the invention of LEDs made possible the supply of monochromatic light, growing plants under only R and B typically determined an abnormal purple-grey colouring, impeding the visual assessment of plant health. Since miscoloured plants were not appealing for consumers, with the aim of improving their appearance as fresh food for Space missions, scientists of the National Aeronautics and Space Administration (NASA).

Lettuce was the first and most investigated crop at the beginning of research on green light, at the NASA Kennedy Space Center (FL, USA), assessing the effects of G addition to a R and B background compared to traditional lamps. In preliminary tests, the inclusion of 5 % G did not exert a relevant impact on leaf photosynthesis and plant growth (Kim et al., 2004; Table 1), while inputs over 50 % resulted in growth inhibition (Kim et al., 2003; Table 1). Specifically, in the latter test four light sources were compared: red and blue LEDs (RB), red and blue LEDs with green fluorescent lamps (RBGf), cool white fluorescent lamps (CWF), and green fluorescent lamps (Gf), providing G at 0 %, 24 %, 51 %, and 86 % of total PPFD (136 μmol m^{-2} s^{-1} in all treatments). At equal light intensity, plants under RBGf (corresponding to 24 % G) showed the greatest leaf area and the highest fresh and dry weight (and a better aesthetic appearance), and under Gf (86 % G) the lowest values of growth parameters, confirming that, although R and B are more efficient in powering photosynthesis, G may promote carbon assimilation in the deeper mesophyll and the inner leaves (as already proved at that time), but high G doses and unbalanced spectra are detrimental. However, since the four light sources implied very broad and different spectral compositions and the specific influence of G over the whole light background could not be ascertained (Kim et al., 2005), and results differed from those of similar experiments (Dougher and Bugbee, 2001), the authors postulated that plant responses could depend on a diverse sensitivity to light quality in the tested cultivars and the diverse light intensity and overall spectra adopted in the tests. Stutte et al. (2009); Table 1) started investigating the hypothesis that antioxidant potential could be regulated by light quality: in the first tests they found that B appeared to regulate the metabolic pathways leading to increased

concentration of bioprotective compounds in leaf tissue, while G had no relevant effect.

Still in lettuce, the comparison of 3 green peaks from LEDs (510, 520, e 530 nm) to white fluorescent (WF) light, at 3 PPFDs (100, 200 e 300 μmol m^{-2} s^{-1}), showed that photosynthesis and plant growth were the highest under G510-PPFD 300, which determined similar plant size and architecture compared to WF, confirming that G can contribute significantly to plant assimilation when provided in sufficient amount (Johkan et al., 2012; Table 1). In lettuce cultivars with red ('Sunmang') and green ('Grand Rapid TBR') leaves, the effects of six R, G, and B LED ratios (R:B 9:1, 8:2, 7:3 and R:G:B 9:1:0, 8:1:1, 7:1:2) were evaluated in growth chamber (Son and Oh, 2015; Table 1). Higher R proportions increased fresh and dry biomass, and also leaf area when combined with B. Replacing B with G (treatments R:G:B 8:1:1 and 9:1:0) improved photosynthesis and plant growth in both the genotypes, while the presence of B promoted the biosynthesis of antioxidants in the red one. In growth chamber, with white light only (W) and W plus B, G, Y, R, or FR LEDs, lettuces showed a normal appearance in W, were compact, dense, and healthy in W*R*, dwarf with larger leaves in WB, sparse and twisted in WY and WFR, and tall with thin leaves under WG (Chen et al., 2016; Table 1). Compared to W control, the addition of R and B improved the fresh weight and chlorophyll and carotenoid content, and both B and G reduced the nitrate accumulation, G increased the soluble sugar content, while FR reduced the biomass and the pigment content, and increased the shoot/root ratio and the biosynthesis of ascorbic acid.

Several studies also highlighted the need of in-depth analyses on the effects of G light on nutritional quality as well as on possible anti-nutritional compounds. In this respect, in end-of-cycle applications to improve post-harvest lettuce quality, among three 24-h treatments of continuous light before the harvest (RB-CL, RBG-CL, and W-CL), the RB treatment limited the nitrate content and stimulated the biosynthesis of phenols and the antioxidant activity (Bian et al., 2016; Table 1). Indeed, adding G to R and B with continuous light (CL) for 48 h before harvest promoted nitrate reductase (NR) and nitrite reductase (NiR) activity at 24 h, subsequently, it reduced the expression of related genes during CL (Bian et al., 2018; Table 1). Compared with R and B, G supplementation increased NR, NiR, glutamate synthase and glutamine synthetase activities. On these bases, light exposure to RB light in preharvest stage is a potential tool to improve leaf quality in lettuce. Li et al. (2021) found that the addition of G during plant cultivation increased the nitrite content and promoted its reduction to ammonium through the activation of NiR gene expression and enzyme activity in lettuce. On these bases, recent research investigated the existence of interactions between G light and nitrogen (N) supply on N metabolism in lettuce, revealing that both regulate the assimilation, protein biosynthesis, and biomass accumulation, even though plant response to their combined effects can be cultivar-specific (Liu et al., 2024). In general, the N availability and G dose showed a synergistic effect on NR and glutamine synthetase/glutamate synthase (GS/GOGAT) cycles and as N supply increased, glutamate dehydrogenase (GDH) activity declined. Biomass accumulation and protein content and GS/GOGAT activity were highest at G 30 % and N 10.5 mmol/L. However, it is worth noting that, by investigating the effects of supplementation of a LED B-R-FR basal spectrum (PPFD 300 μmol m^{-2} s^{-1}) with 10 % G, in lettuce in controlled environment, Viršilė et al. (2020) highlighted a different genotype response to light *stimuli* in terms of nutritive primary metabolites (nitrite, amino acid, organic acid, and soluble sugars) depending on the leaf pigmentation, and a more positive impact in a red than a green cultivar.

All together, these results suggest that supplementing G to W and R-B light background can improve the plant performance in lettuce, however the presence of G seemed to be beneficial over a certain minimum threshold and detrimental over a certain percentage of total radiation (i.e., 50 % of PPFD), and the mixing ratio with R and B seems to be very important for achieving normal growth in leaf lettuce (Ohashi-Kaneko et al., 2007; Table 1). This range of effectiveness would explain how some experiments gave conflicting results, as the addition of low G doses (e.g., 10 % of 150 μmol m^{-2} s^{-1} PPFD, corresponding to 15 μmol m^{-2} s^{-1}) that did not exert any observable effect on the growth of lettuce (Kang et al., 2016). Meng et al. (2020) postulated that G could be effective in suppressing the promotion of growth and secondary metabolism induced by B depending on the B photon flux density and that in some experiments the observed effects on plant growth could be attributed to diminishing B rather than increasing G. They demonstrated the dependence of G effects on the B PFD using a wide range of B PFDs (0–100 μmol m^{-2} s^{-1}) and high G PFD (60 μmol $m^{-2}s^{-1}$), in accordance with several studies showing minimal effects of G under low B.

Artificial lighting is typically static in indoor production; however, plants could have different light requirements, in terms of intensity, photoperiod and spectrum, in the different phenological phases. Meng and Runkle (2020) characterized the time-dependent responses of a red lettuce to LED treatments (20-h photoperiod, growth chamber). Plants received 6 static treatments with the same PPDF (subscripts, in μmol m^{-2} s^{-1}) WW_{180}, R_{180}, $B_{20}R_{160}$, $B_{20}G_{60}R_{100}$, $B_{20}R_{100}FR_{60}$, or B_{180}, from day 0–11, then they were transferred to 36 temporal spectrum alternations. In the B20 background, partially replacing R with G ($B_{20}G_{60}R_{100}$) did not influence FW at the middle of the cycle while reduced it at the harvest. The treatments applied before light switch influenced the final weight but, in comparison, the effects of treatments applied later were stronger. The authors concluded that some phenotypic responses of lettuce to light quality depend on time and that sequential light quality treatments had cumulative effects on growth. This creates opportunities for dynamic light recipes in the distinct growth phases, to control desirable traits.

It has been proved that, in general, plant response to light spectrum also depends on the light intensity. In wheat (*Triticum aestivum* L.) plants grown under continuous white fluorescent light (257 μmol m^{-2} s^{-1} total PPFD, 49 μmol m^{-2} s^{-1} G) integrated with 4 different densities of LED green light, increasing G progressively reduced the days for the heading, with the earliest production under the highest dose (32.0 days after the emergence) (Kasajima et al., 2008; Table 1). A logarithmic function fitted well the relationship between G dose and developmental rate, and results of the principal component analysis (PCA), adopted to analyse the impact of light treatments on 17 growth and morphological traits, suggested that the development of wheat was promoted by the green light. In wheat, radish (*Raphanus sativus* L.), and lentil (*Lens esculenta* Moenh.), the effect of LED spectra on the antioxidant properties of sprouted seeds was evaluated in controlled conditions (PPFD 100 μmol m^{-2} s^{-1}; 12 h photoperiod; 27°C), comparing 5 treatments: 638 nm (L1); 455, 638, 669 and 731 nm (L2, basal components); basal+ 385 nm (L3); basal+ 510 nm (L4), basal+ 595 nm (L5) (Samuolienė et al., 2011; Table 1). The antioxidant activity and antioxidant compounds content in seeds germinated in the dark were lower than those in LED light. Radish accumulated more phenolic compounds and were less sensitive to light spectrum compared to wheat and lentil and showed higher free-radical scavenging capacity. The integration of basal light with G enhanced the antioxidant properties of sprouted seeds in wheat and lentil using 510 nm diodes, and in radish using 595 nm (amber light). Comparing 6 R-B-G spectra in spring wheat, grown in growth chamber in space-oriented experiment, showed later that seed production was higher in R:B:G 80:10:10 and did not further increase when G exceeded 10 % of total radiation, suggesting that also wheat plants presumably benefit of only a limited amount of G (Shen et al., 2020; Table 1).

The influence of 8 spectra from LEDs, cool (CW), neutral (NW) and warm (WW) white, narrow band R, B, and G, alone and in the combinations RB (86.3:12.0) and RGB (63.4:22.9:1.7), at 200 and 500 μmol m^{-2} s^{-1}, was studied in 7 crops (lettuce, radish, cucumber, tomato, pepper, wheat and soybean) in growth chamber (Snowden et al., 2016; Table 1). Dry matter accumulation was generally unaffected under low light and only slightly influenced at high light by G, except for radish, in which it was reduced by G from 22.9 % upwards. However, increasing G increased plant leaf area in cucumber, specific leaf area in pepper, stem length in tomato, pepper, soybean, and lettuce, and petiole length in

radish and soybean. Since in dense canopy crops the quota of green light generally rises in the more internal leaf positions, this evidence is consistent with morphological changes associated with the plant need to enhance the light interception (i.e., stem and petiole lengthening, leaf expansion) to compensate the growth deficit determined by low B or high G proportion. Consistently, these effects were greater at lower PPFD. On these bases, G light addition could be used to enhance growth in responsive species. However, investigating the effect of the fraction of B (10–30 %) and G (0–50 %) at 200 and 500 μmol m^{-2} s^{-1} in lettuce, cucumber and tomato, Kusuma et al. (2021) found species-dependent responses to light spectrum. As expected, increasing the fraction of B generally reduced the leaf area and dry mass. By contrast, changes in the fraction of G had minimal effects on leaf area and dry mass in lettuce and cucumber, and increased stem and petiole length in cucumber and tomato.

In basil (*Ocimum basilicum* L.) and Chinese cabbage (*Brassica campestris* L.), G reduced the plant growth compared to R or B light (Fan et al., 2013; Table 1). In Chinese cabbage, the chlorophyll concentration in G was lower compared to B but similar to or slightly higher than R, and the photosynthetic efficiency was lower than under B light. In basil, four LED treatments were tested in two cultivars (Lettuce Leaf and Red Rubin): high R and high R:FR, high R and low R:FR, moderate B and R and low R:FR, and high B, G, R:FR and 1 % ultraviolet, compared to fluorescent light (high B, G, R:FR) as Control in the growth chambers (PPFD 200 mmol $m^{-2}s^{-1}$ for all treatments) (Bantis et al., 2016; Table 1). Total biomass was significantly greater, but leaf area was lower in presence of G compared to Control. G light influenced the total phenolic content, although the effect was variable in the cultivars. Still in basil, the progressive replacement of R or B with G was tested in a green and a purple cultivar (Dou et al., 2019; Table 1). Compared to RB 76:24, photosynthesis was unaffected by G integration in green plants, while remarkably increased at increasing G rate in the purple ones (+45 % in R:B:G 74:16:10 and +59 % in 44:24:32). In both cultivars, combining G to a B-R background at relevant rate (i.e., 32 % and 45 %) promoted stem elongation. However, while in the green genotype none of the spectra influenced leaf traits and plant yield, in the purple one they both reduced leaf thickness and yield, and the second one (45 % G) also caused petiole lengthening. Polyphenols content and antioxidant activity decreased with 10 % and 45 % G in green basil, and with 32 % and 45 % G purple basil. The overall results highlighted that the influence of G depends on the plant genotype and the prevailing pigment composition of leaf tissue, and that the choice of G rate needs to consider the genotype sensitivity. Afterward, the authors tested different proportions (in %) of RB (R88:B12, R76:B24, and R51:B49) and RBG, with the same B doses (R44:B12:G44 and R35:B24:G41), in green and purple basil, green and red mustard, and green and red kale, in growth chamber (PPFD 224 μmol m^{-2} s^{-1}, 16-h photoperiod) (Dou et al., 2020). Including a high G dose (R44:B12:G44) promoted stem elongation in green genotypes of basil and mustard, while the influence of G on secondary metabolites was species dependent. Based on biomass production and nutritional and nutraceutical properties, low B and G integration on a white light background is recommended for these crops. This recommendation is also valid to 'photomodulate' volatile organic compounds (VOCs) and aroma in sweet basil. Indeed, comparing G, B, R, and polychromatic light (W - R:G:B, 1:1:1) supplemented at 250 μmol m^{-2} s^{-1} (5 h d^{-1}) to greenhouse ambient light, Lauria et al. (2023); Table 1) found that in both a green ('Tigullio') and a red ('Red Rubin') cultivar light integration did not alter plant biomass compared to the sunlight control. Conversely, monochromatic lights selectively modulated metabolomics profile in the green and red leaves (e.g., B increased polyphenols in 'Tigullio', and G reduced the anthocyanin cyanidin-3-coumaroil-glucoside in 'Red Rubin'). The volatilome profile analysis revealed strong spectral-dependent alterations: for instance, eugenol (one of the major toxic compounds in basil, conferring the typical clove flavour) decreased in all the LED treatments. The overall results clearly evidenced that monochromatic light integration is a valid tool to trigger targeted secondary metabolism responses. In this respect, the balance between G and B radiation was proven to temper both the total amount and the profile of phytochemicals also in plants of tea (Zheng et al., 2019b). Indeed, B and G lighting in the dark period increased the content of ascorbic acid, anthocyanins, catechins (related to plant defence and stress responses) and improved leaf photosynthesis and plant growth under low white light conditions during daytime. Also in this crop, results highlighted the effectiveness of targeted treatments to improve taste and nutraceutical quality of the product.

As the prevailing colour reflects a different pigment composition and the related antioxidant activity of plant tissues, Izzo et al. (2019) studied the influence of four light spectra, 100 % white (W) or red (R), 50–50 % RB, and 33–33–33 % RGB (12-h photoperiod, daily light integral 10.8 mol m^{-2}), on green and red leaf cultivars of *Atriplex hortensis*, an edible leaf crop recently reappraised for food production in controlled environment for the good nutritional and nutraceutical properties (mainly due to the content of betacyanins, anthocyanin-homologues with high antioxidant activity). In both cultivars, the addition of G was detrimental for dry mass accumulation, and it was irrelevant for betacyanins in the green cv. while reduced it compared to RB and increased it compared to W in the purple cv. In red plants, betacyanin concentration was two orders of magnitude greater than in the green ones and increased as the B light increased, hence, in the view of boosting antioxidant properties of this crop through light spectrum modulation, red genotypes could be more promising.

About the controversial evidence reported in literature on the effects of G light in vegetables, Kaiser et al. (2019) hypothesized that, as most experiments were carried out on small plant species with compact size and short life cycles in growth chamber, a positive impact related to the high penetration capacity of G in the leaf mesophyll and in the canopy could have been unexpressed or may have been disregarded. Hence, they tested an increasing G rate (7, 20 and 39 %) added to R-B light (171 μmol $m^{-2}s^{-1}$) on tomato, integrating the greenhouse sunlight background. The G addition boosted the biomass accumulation and fruit production only at 39 % G (+6.5 % than in R-B integration), while only a trend to higher values of plant height, specific leaf area, and aerial biomass occurred at lower rates. Gas exchange and pigment content were unaffected by light spectrum, while Chl a:b ratio and carotenoids increased with the G intensity in middle leaves. These results showed that the partial replacement of R with G on a sunlight background improved growth in tomato (as a model greenhouse crop with dense canopy and long cycle), and highlighted a synergistic action of these wavebands, as the combined effects on photosynthesis were more than the sum of their single impact.

Genotype-dependent response to light spectrum was also described in spinach. Different wavelengths at varying ratios, red-blue (R4:B1), red-blue-green (R5:B2:G3) and red-blue-green (R1:B1:G1), at 190 μmol m^{-2} s^{-1}, were investigated in an indoor system (Nguyen et al., 2021; Table 1). Results showed that the addition of G to R and B could reduce the plant growth and leaf quality of spinach over a certain threshold and that the best growth parameters, photosynthetic pigments, leaf traits and quality were observed in R4:B1 treatment, but not for the organic acid content.

Recently, Chen et al. (2024) performed an in-depth comparative meta-analysis to determine the relative effect of green light for a range of plant traits (e.g., fresh and dry weight and leaf area), as the ratio between the value attained under a R-B background plus G, divided by the value obtained with the background light only (at the same intensity). Based on the output of the analysis of 136 datasets on 17 crops, including common leaf and fruit vegetables (e.g., lettuce, basil and tomato), the authors concluded that G light can be equally effective than R and B in promoting plant biomass production. This statement was based on a deep evaluation of both direct effects on carbon assimilation and indirect effects on photomorphogenesis, and also detected a more efficient action of longer (580–600 nm) compared to shorter (<530 nm) wavelengths and a species-specific sensitivity to green. On this basis, the

authors suggest reconsidering G as a valuable component of lighting recipes in horticulture.

7. Conclusion and future perspectives

This review of studies on the influence of green light on physiological, morphological and metabolic processes, and transcriptional regulation in vegetable and herbaceous crops highlights the importance of this wavelength for plants, in both natural environment and protected cultivation. Although research on spectral dependence of these processes is mainly focused on the effects of R and B combinations, the application of G wavelengths has been drawing increasing attention in basic research as well as for crop production purposes. It is now ascertained that green light can be involved in fine-tuning of plant processes in coordination with R and B, may function as a shade signal and drive acclimation to low light conditions, and can promote reaction to biotic and abiotic stress. Hence, including green light as additional component in multispectral and dynamic recipes of artificial light represents a promising tool to improve plant growth and crop yield and product quality in greenhouse horticulture and controlled environment agriculture. Understanding the mechanisms underlying the plant response to green light and characterizing the sensitivity of different crops and genotypes would allow to better design the plant density and architecture, allowing a better interception of natural and artificial light, and to modify the greenhouse light environment, enhancing the overall crop performance.

CRediT authorship contribution statement

Paradiso Roberta: Writing – review & editing, Writing – original draft, Supervision, Methodology, Data curation, Conceptualization. **Cocetta Giacomo:** Writing – review & editing, Methodology, Data curation. **Proietti Simona:** Writing – review & editing, Methodology, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

RP proposed the topic and wrote the article outline. RP and SP performed the literature review. RP, GC and SP contributed to elaborate the bibliographic sources, to write the article and to prepare figures.

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