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Review

Ménage à trois: light, terpenoids, and quality of plants

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In controlled environment agriculture (CEA), light is used to impact terpenoid production and improve plant quality. In this review we discuss various aspects of light as important regulators of terpenoid production in different plant organs. Spectral quality primarily modifies terpenoid profiles, while intensity and photoperiod influence abundances. The central regulator of light signal transduction elongated hypocotyl 5 (HY5) controls transcriptional regulation of terpenoids under UV, red (R), and blue (B) light. The larger the fraction of R and green (G) light, the more beneficial the effect on monoterpenoid and sesquiterpenoid biosynthesis, and such an effect may depend on the presence of B light. A large fraction of R light is mostly detrimental to tetraterpenoid production. We conclude that light is a promising tool to steer terpenoid production and potentially tailor the quality of plants.

Highlights

Light spectral composition regulates terpenoid biosynthesis, abundances, and chemical diversity in both aboveground and belowground organs, thus impacting the nutritional and medicinal content, aroma, flavor, and color of plants.

Red and blue (B) light regulation of terpenoid biosynthesis is mutually dependent, and a light spectrum >50% of red (R) tends to be detrimental to the biosynthesis of various terpenoids.

The transcription factor elongated hypocotyl 5 (HY5) plays a central role in UV, R, and B light signaling regulating terpenoid biosynthesis.

Beside HY5, MYB and trichome-specific transcription factors play a role in UV light signaling affecting terpenoids.

The affair between plants, specialized metabolites, and light

Plants are used globally by humans as a source of nutrition, ornamentation, delight, and medicine. Approximately 25% of the pharmaceutical drugs worldwide are extracted from **plant specialized metabolites (PSMs)** (see Glossary), causing high demand for **medicinal plants** [1]. This high demand can be fulfilled by making use of efficient cultivation systems, which at the same time allow prevention of issues regarding environmental pollution, contamination and adulteration, quality control, and inconsistency of chemical profiles [2]. **CEA** offers a feasible way to mitigate these issues by fully controlling environmental factors, including light, temperature, CO_2, water, nutrients, and air humidity [2,3].

PSMs include a plethoric group of compounds derived from the primary metabolic pathways, and are involved in most important physiological processes of a plant, including growth, development, and survival in an environment that is often hostile [4]. To date, more than 200 000 PSMs have been described and classified into three main groups: phenolics, **terpenoid**s (terpenes and steroids), and alkaloids [5]. This outstanding diversity of PSMs has been described to result from common building units (isoprene and shikimate precursors). PSM diversity is also due to biosynthetic genes from large gene families encoding homologous enzymes, enzymes producing and modifying multiple products from the same precursor, and biosynthetic differences in terms of time and location (organ/tissue-specific) [6]. Most PSMs are involved in the nutritional value, flavor, aroma, and color of plant parts (leaf, stem, root, rhizomes, blossoms and flowers, fruit, and seeds), and have found their use in human health-promoting substances [7].

Among the three groups of specialized metabolites, terpenoids are the largest family of compounds with physiological relevance (~80 000 known structures, of which 30 000 are found in plants) [8]. Terpenoids (Box 1) are ubiquitous in all living organisms as essential membrane components,

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Box 1. Terpenoids: structure, occurrence, and allocation

Structure

Terpenoids, also known as isoprenoids, are a group of specialized metabolites consisting of a single or multiple five-carbon (C_5) isoprene molecule(s). Isoprenoids may present different moieties such as glycosylation, prenylation, ring closures, unsaturation, functional groups, and oxidation [122]. When the structural skeleton does not include any modification, therefore being a hydrocarbon, the molecule is known as terpene [123]. Here we use 'terpenoid' as an umbrella term which includes terpenes and their derivatives.

Terpenoids can be classified according to the number of isoprene (C_5) present in the molecule skeleton: one isoprene is a hemiterpenoid (C_5), two a monoterpenoid (C_{10}), three a sesquiterpenoid (C_{15}), four a diterpenoid (C_{20}), six a triterpenoid (C_{30}), eight a tetraterpenoid (C_{40}), and more than eight polyterpenes ($C_{[n>40]}$) [123]. Other examples include homoterpene (irregular acyclic C_{11} or C_{16}) and sesterterpenoid ($C_{21,22,25,26,27}$) [124]. Terpenoids are subclassified based on the arrangement of the molecular skeleton and the presence of various moieties/modifications. For instance, monoterpenoids can be subclassified as acyclic, monocyclic, and bicyclic [123]. Similarly, sesquiterpenoids are also found in the same subclasses as monoterpenoids, but also as tricyclic [123] and sesquiterpenoid lactones (artemisinin) [46]. Diterpenoids are subclassified as bicyclic, tricyclic (tanshinone) [28], tetracyclic, and macrocyclic (taxol) [15,125]. Triterpenoids are subclassified as acyclic, monocyclic, bicyclic, tricyclic, tetracyclic (cucurbitacins) [126], pentacyclic, tetranortripenoids (limonoids) [127], and triterpene glycosides (saponins) [128,129]. Finally, meroterpenoids (cannabinoids) form another subclass of terpenoids with phenolic moieties [130].

Occurrence and allocation

The occurrence of terpenoids in various vegetative and reproductive plant organs is mostly associated with their physiological function and is influenced by the environment. In most cases, terpenoids are produced, accumulated, and contained (preventing autotoxicity) in the cells of specialized structures with secretory activity [10,131]. Terpenoids are commonly found in internal (laticifers, resin ducts, oil glands) and external (colleters, and trichomes) secretory structures [131].

Internal secretory structures are found in the xylem, phloem, cortex, and parenchyma; such structures are found in the cytoplasm and contain oils, oleoresins, crystals, and others [131]. For instance, laticifers (latex producers) and resin ducts are internal secretory structures in conifers that allow the transport of oleoresins (mixtures of mono-, sesqui-, and diterpenoids) from the production site to the site of mechanical damage through an interconnected canal system [10]. Resin ducts can be found in roots, stems, leaves, and flowers [131]. Other similar structures include resin cells and blisters, generally absent or at very low densities, and can be induced upon biotic stress [10]. Oil cavities are also internal secretory structures that can be found in the leaves, coupled with epithelial cells, but also throughout the whole plant, producing essential oils [131].

External secretory structures are tightly associated with the epidermal layer, and can be found in most ferns, angiosperms, and gymnosperms. Glandular trichomes are external secretory structures, consisting of multicellular (glands) epidermic extensions, found in bud scales, leaves, stems, and reproductive organs, producing and accumulating a vast variety of terpenoids [10]. Glandular trichomes act as minuscule factories of organic compounds composing essential oils [132]. Other specialized glandular trichomes include stinging hairs and colleters, which are also external secretory structures producing resinous substances and essential oils that act as a protective barrier preventing desiccation and biotic attack [131]. Some popular examples of plants with glandular trichomes producing terpenoids include *Cannabis sativa* L. [133], *Solanum lycopersicum* [134], *Artemisia annua* L. [135], and *Ocimum basilicum* [136]. Essential oils are composed of 90% terpenes/terpenoids; hence, oil cavities, glandular trichomes, and colleters are important sites for terpenoid biosynthesis [137]. It is important to mention that the terpenoids produced *in vivo* are termed volatile or ethereal oils, while essential oils is the term used when the volatile oils have been extracted [131].

including eukaryotes (e.g., cholesterol), protozoa (biogenetic precursor of cholesterol, the triterpene cycloartenol or the pentacyclic triterpene tetrahymanol), and prokaryotes (membrane polyterpenic surrogates: hopane, bacteriohopane, α-,Ω-dipolar carotenoids, tricyclopolyprenols, and isoarborinol) [9]. These metabolites can function as herbivore deterrents, allelopathic/toxic molecules, attractants of pollinators and beneficial predators, hormone precursors (gibberellins, cytokinins, brassinosteroids, strigolactones, and abscisic acid), thermotolerance molecules (isoprene and monoterpenes), electron carriers (plastoquinone and ubiquinone), and pigments with photosynthetic, photoprotective, and/or antioxidant activity (phytol in chlorophyll and carotenoids) [10–14]. From an anthropogenic perspective, the use of terpenoids is economically important in various industries: namely, pharmaceutical, cosmetic, fragrance, and food. Some remarkable examples include applications in flavor and aroma (menthol), antimalarial (artemisinin) and anticancer (taxol), and production of biomaterials and biofuels (oleoresin or crude turpentine) [15].

Glossary

Blue (B) light: photons of wavelengths in the range 400–500 nm.
Cannabinoids: meroterpenoids containing a phenolic moiety that can be found, but not exclusively, in *Cannabis sativa* L. Two examples with health benefits for humans are Δ-9 tetrahydrocannabinol (THC) and cannabidiol (CBD).
Controlled environment agriculture (CEA): any type of plant production system in which climate conditions are partially or completely controlled. This term includes indoor systems, greenhouses, vertical farms, and plant factories.
Daily light integral (DLI): the cumulative amount of photons of wavelengths in the range 400–700 nm incident on one square meter over a 24 h period.
Elongated hypocotyl 5 (HY5): a basic leucine zipper (bZIP)-type transcription factor described as a master regulator in light-induced pathways involved in the interaction with all photoreceptors sensing photons from the UV-B to the far-red spectra.
Far-red (FR) light: photons of wavelengths in the range 700–800 nm.
Green (G) light: photons of wavelengths in the range 500–530 nm.
Medicinal plant: any plant the organs and derivatives thereof contain specialized metabolites with therapeutic properties that can be developed into pharmaceutical, cosmetic, and nutritional formulations.
Phytochrome interacting factors (PIFs): a family of transcription factors containing a basic helix–loop–helix (bHLH) domain that physically interacts with red and far-red light photoreceptors.
Phytoene synthase (PSY): an enzyme responsible for the first catalytic step in carotenoid biosynthesis.
Plant specialized metabolites (PSMs): also referred to as secondary metabolites, are compounds involved in different plant physiological processes, including plant defense, stress response, growth, and development. Many of these compounds have been anthropogenically used for the development of applications in pharmaceutical, textile, food, flavor, and aroma industries.
Quality of plants: an anthropogenic concept determined by the interaction between the phenotypes of plants and the senses of humans, which defines acceptability, fitness for consumption, and use.

Light is considered as a crucial environmental factor to produce specialized metabolites in plants [1]. Because CEA allows the modulation of light properties [3], it has been used to regulate specialized metabolites in plants so that they yield more nutritious, healthier, and more appealing produce [1,2,7,16,17]. Light spectrum affects the production of all PSMs [1]. Plants perceive light spectra via five groups of photoreceptors that activate signaling pathways determining morphological, physiological, and metabolic responses [18]. These photoreceptors are categorized according to their sensing spectral range: phytochromes (PHYs) sense mostly in the region of 600–750 nm but also 400–485 nm; cryptochromes (CRYs), phototropins (PHOTs), and Zeitlupe/flavin-binding Kelch/LOV Kelch Protein (ZTL/FKF1/LKP2) in the region of 350–500 nm; and UV resistance locus (UVR8) at 280–350 nm [18–20]. Light spectrum has a role in regulating the biosynthesis and accumulation of terpenoids which are involved in the **quality of the plant** (determining aroma, flavor, color, and medicinal and nutritional properties). Light spectrum can affect the biosynthesis of terpenoids by upregulating and downregulating various enzymes of the biosynthetic pathways [1,21–24]. For example, in young grape leaves terpene synthase (TPS) activity increased under low **UV-B** (8.25 μW cm^{-2} for 16 h/d) compared with no and high UV, leading to augmented contents of membrane terpenoids, including stigmasterol, lupeol, and sitosterol [25]. Moreover, after exposing *Prunus persica* L. leaves and fruits to UV-B for 48 h, gene transcript levels of two TPSs changed (PpTPS1 decreased and PpTPS2 increased). Consequently, reducing and enhancing the content of linalool (sweet, floral, and alcohol notes in flavor quality) and (*E,E*)-α-farnesene (woody, citrus, green, and fruity notes), respectively [26]. Furthermore, **red (R) light** stimulates triterpenoid biosynthesis in plantlets of *Aquilaria agallocha* grown *in vitro*, specifically regulating genes related to the production of curcubitacin E and I (antitumoral) in *Aquilaria* and *Gyrinops* trees [27]. By contrast, light spectra containing >60% **blue (B) light** downregulate the expression of six biosynthetic terpenoid genes, and therefore have a suppressive effect, involved in the production of the medicinal abietane diterpene tanshinone IIA in hairy roots of *Salvia miltiorrhiza* [28].

Light intensity and photoperiod also affect the biosynthesis of terpenoids. Decreasing solar light intensity (maximum 1600 μmol/m^2/s) by 16% or 33% using shading nets enhanced the production and accumulation of two pentacyclic triterpenoids with several pharmacological activities (ursolic acid and oleanolic acid) in *Glechoma longituba* aboveground plant tissue [29]. Moreover, in *Lippia gracilis* grown *in vitro*, a low light intensity (26 μmol/m^2/s) resulted in a more complex terpenoid composition (more constituents detected) when compared with higher light intensities (51–130 μmol/m^2/s) [30]. Highest terpenoid production in *G. longituba* was associated with a **daily light integral (DLI)** ≤19 mol/m^2/d, while in *L. gracilis* more diverse terpenoid profiles were associated with a DLI that occurs at 2 mol/m^2/d. In addition, it was also observed that terpenoid profiles significantly increased as the DLI values increased 1–4 mol/m^2/d in *Lippia alba plantlets* grown *in vitro* [31].

The ubiquity, physiological relevance, and biological activity of terpenoids and their involvement in the quality of plant-derived products that are cultivated and consumed by humans make these molecules a target to understand plant behavior. The various applications of terpenoids, and therefore their high demand in the global market, mean that these metabolites are often chemically synthesized [32]. To produce these compounds in a 'greener' way, metabolic engineering has been exploited as a technological approach, allowing the control of environmental conditions and cell growth, regulation of biosynthesis, and extraction [15,32,33]. However, the metabolic pathway of terpenoids is rather complex, making genetic modification approaches difficult and resource-intensive [32]. Alternatively, harnessing the plants metabolic machinery to enhance the production of terpenoids by using light modulation offers an easier, controllable, and noncontroversial option [34]. In this review we synthesize recent developments on light regulation of

Red (R) light: photons of wavelengths in the range 600–700 nm.
Terpenoids: also known as isoprenoids, a group of specialized metabolites consisting of a single or multiple five-carbon (C_5) isoprene molecule(s). Isoprenoids may present different moieties such as glycosylation, prenylation, ring closures, unsaturation, functional groups, and oxidation. Without any structural modification (hence a hydrocarbon), the molecule is known as a terpene. In this review we use 'terpenoid' as an umbrella term including terpenes and their derivatives.
UV-A light: photons of wavelengths in the range 315–400 nm.
UV-B light: photons of wavelengths in the range 280–315 nm.
UV-C light: photons of wavelengths in the range 100–280 nm.
White (W) light: photons of wavelengths in the range 400–700 nm.
Yellow (Y) light: photons of wavelengths in the range 530–600 nm.

terpenoid biosynthesis and accumulation in different plant organs. Furthermore, we convey a detailed analysis of terpenoids that have been described to be affected by light and are involved in the organoleptic, nutritional, and medicinal quality of plant organs.

Raison d'être: a connection between terpenoids and quality of plants

Quality of plants is an anthropogenic concept determined by the interaction between the phenotype of plants and the senses in humans, defining acceptability and appropriateness for consumption and use. Quality is assigned based on morphophysiological characteristics, including water and mineral content, tissue appearance and consistency, and PSM composition [35]. PSM composition can be the determinant of aroma, flavor, taste, pigmentation, medicinal, and nutritional properties in plants, and terpenoids are protagonists in this narrative (Figure 1).

A substantial part of a plant's odor consists of volatile compounds produced via terpenoid biosynthetic pathways [36]. All plant parts produce volatile terpenoids, and their emission to the environment functions as an environmental cue for attraction of pollinators, deterring predators, and plant–plant communication [37]. Also, volatile terpenoids are important stress regulators because they can act as antioxidants by quenching photo-oxidative stress, as well as stabilizing pigment–protein complexes resulting in more thermotolerant thylakoid membranes [38]. Volatile terpenoids are relevant for the quality, and consumer acceptance thereof, of various plant-derived commodities (fruits, leaves, and flowers). Quality of plants can be evaluated via aroma composition, which also influence flavor (taste and olfaction) [39]. Volatile terpenoids are predominant aroma components in *P. persica* (linalool), *Citrus x sinensis* [(+)-valencene], *Fragaria x ananassa* (linalool and nerolidol), and *Camellia sinensis* (linalool, β-ocimene, β-pinene, and geraniol) [40–42]. In flowers, volatile terpenoids (monoterpenoids, sesquiterpenoids, and diterpenoids) have been researched in the composition of over 556 floral scents [37,43].

Carotenoids are non-volatile terpenoids essential for the photosynthetic apparatus acting as accessory pigments, photoprotectors, antioxidants, and hormonal precursors [44]. Carotenoids can determine the visual, nutritional, and medicinal quality of plant-derived commodities, including leaves, fruits, stems, flowers, and underground organs [45]. Examples of carotenoids include carotenes (α-, β-, γ-carotene, and lycopene) and xanthophylls (zeaxanthin, β-cryptoxanthin, and lutein), which are not only responsible for the yellow–orange pigmentation in plants, but also determine provitamin A, antioxidant, and anti-inflammatory activity [16,44]. Another example is the sesquiterpenoid lactone artemisinin, which determines the medicinal quality of *Artemisia annua* L., as it has potent antimicrobial, antitumoral, and other pharmacological activity [46]. Also, the medicinal quality of the rhizomatous plant *Curcuma longa* is derived mainly from monoterpenoids and sesquiterpenoids produced in its rhizome [47].

In many plants terpenoids provide aroma, flavor, and determine medicinal properties. Such is the case for *Cannabis sativa* L., inflorescences, where more than 120 terpenoids (myrcene, β-caryophyllene, α-humulene, geraniol, linalool, β-pinene, and others) are responsible for the characteristic aroma and flavor, but also for enhancement of the therapeutic properties (analgesia, antimicrobial, and anti-inflammatory) by interacting with other terpenoids (**cannabinoids**) [48,49].

Regulation of terpenoids by light

As of today, the combination of cultivation systems with advanced lighting technologies and plant production have allowed us to explore and better understand terpenoid plasticity upon modulated light environments. In horticultural and plant physiological research, light is taken as a factor that can influence plant growth, morphology, physiology, as well as specialized metabolism via quality (spectrum), duration (photoperiod), and quantity (DLI). We discuss the recent insights

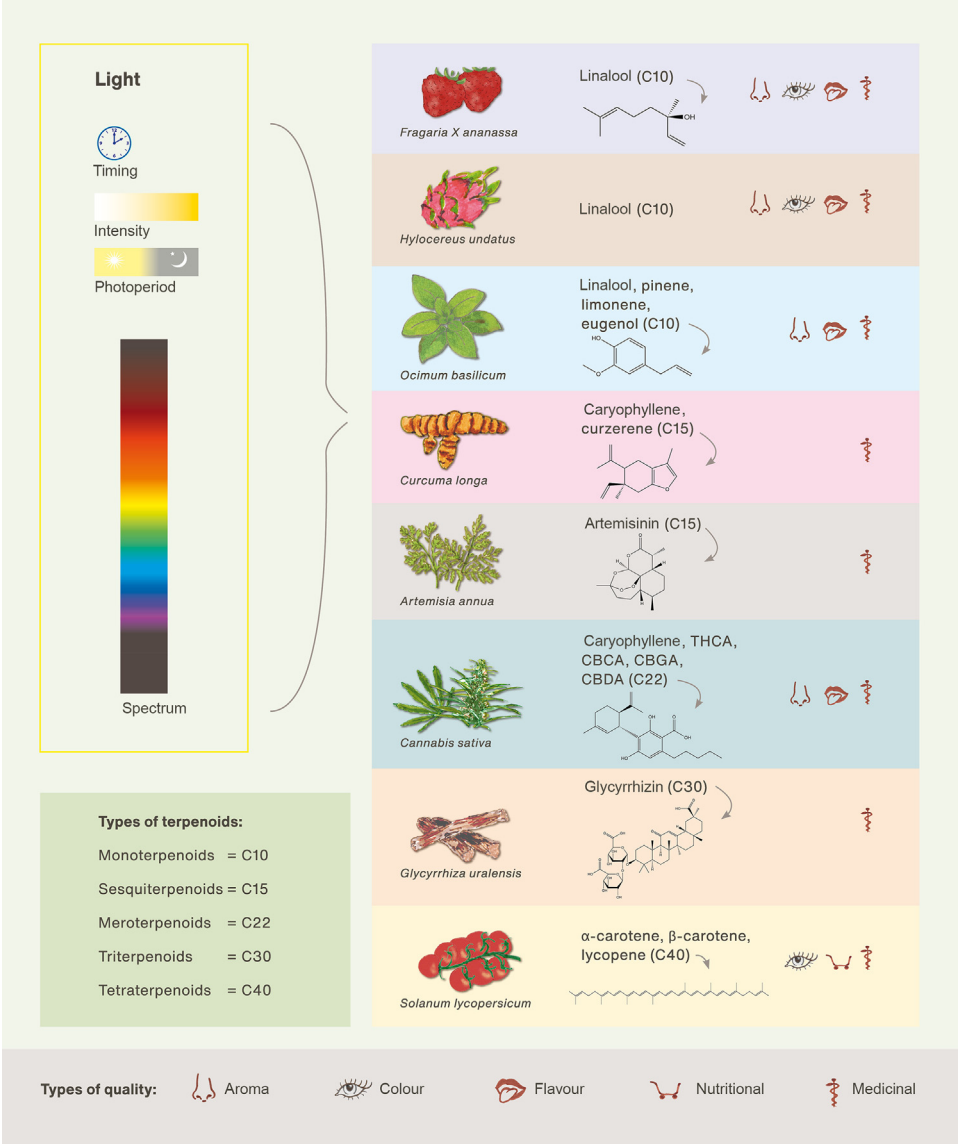

Figure 1. Light as a tool to steer the production of various classes of terpenoids in different plant organs, and their role in determining the quality of plants. Abbreviations: CBCA, cannabichromenic acid; CBDA, cannabidiolic acid; CBGA, cannabigerolic acid; THCA, Δ9-tetrahydrocannabinolic acid.

regarding light-regulated terpenoid profiles and abundances, with diverse occurrence and allocation, and their slightly different underlying mechanisms based on organs of several plant species.

Fruits

Tomato fruits are produced and consumed worldwide due to their nutritional value which is given by the presence of terpenoids (carotenoids and tocopherols), phenolic compounds, and other nutrients [50]. The most abundant carotenoids in tomatoes are β-carotene and lycopene, consumption of which has been related to various health-promoting properties [50]. Aside from the

nutritional and medicinal quality, lycopene is also involved in the visual quality of tomatoes (Figure 1) [51]. Light spectra during cultivation, so pre-harvest, can affect tomato fruit carotenoid composition. Exposing tomato plants after anthesis to natural light supplemented with monochromatic blue light resulted in higher content of the tetraterpenoids lycopene and β-carotene in tomato fruits compared with supplementation with monochromatic R light (50 μmol/m^2/s, 12 h/day) [52]. Although lutein levels were also increased by B and R light, they progressively decreased over time after anthesis [52]. Postharvest light spectra can affect terpenoid accumulation in tomato fruits [50]. Continuous postharvest exposure to supplemental monochromatic B light significantly increased the content of lutein and β-carotene, while α-carotene was increased by supplemental monochromatic B and **green (G) light** compared with other treatments [dark, R, **white (W) light**, and **far-red (FR) light**] [50]. Moreover, lycopene accumulation can be more pronouncedly increased with supplemental monochromatic FR and G light, compared with W, B, and R light [50]. Complementarily, mature green-stage tomatoes stored under R light (0.005–0.023 μmol/m^2/s, 15 min/day) showed higher accumulation of lycopene compared with low R:FR and darkness, and such improvement could be reversed by the application of 15 min of FR light after red light; these changes were not visually obvious in the color of the tomato [53].

Under R light, resulting in a high R:FR ratio, PHY activity is increased, leading to **phytochrome-interacting factor (PIF)** degradation, and inducing the expression of **phytoene synthase (PSY)** genes, via **elongated hypocotyl 5 (HY5)**, which are enzymatic rate determinants in carotenoid biosynthesis (Figure 2) [52]. High levels of lycopene are observed with high PHYs, HY5, and PSY expression levels [52]. Complementarily, B light induces the expression of CRYs to later bind PIFs and E3 ubiquitin-ligase CONSTITUTIVELY PHOTOMORPHOGENIC 1 (COP1), inhibiting and preventing the degradation of HY5 to consequently promote the biosynthesis of lycopene (Figure 2) [21]. R, B, and FR light seem to be indispensable regulators of carotenoid biosynthesis, and their effect depends on the developmental stage. Therefore, deepening our understanding of different R:B:FR ratios is essential to identify suitable light spectra maximizing carotenoid concentrations in the tomato.

Strawberry fruit is an iconic example of the importance of terpenoids for the quality of fruits. The overexpression of a TPS in *F.* X *ananassa* (FaTPS1) leads to increased levels of the sesquiterpenoid germacrene D and can improve resistance to *Botrytis cinerea* in the strawberry (Figure 1) [54]. Moreover, linalool production can be upregulated upon *B. cinerea* infection, while fumigation with linalool can inhibit fungal growth [55]. Flavor composition of strawberry fruits is significantly influenced by a small fraction (0.001–0.01% of fruit fresh weight) of volatile compounds (terpenoids, esters, alcohols, ketones, etc.) [41]. The main terpenoids found in strawberry fruits are menthanethiol, linalool, and nerolidol, although other terpenoids – including α-pinene, β-myrcene, α-terpineol, and β-phellandrene – are present in various cultivars and developmental stages of the fruit [41]. After postharvest exposure to R-enriched light (R film) the terpenoid emission in strawberries was maximally promoted (77% higher than under transparent film), nerolidol being the most abundant [56]. The final step for the biosynthesis of nerolidol and linalool is catalyzed by *F.* X *ananassa* nerolidol synthase 1 (FaNES1) [56,57]. Consistently with the emission levels of nerolidol, under R film the expression of FaNES1 was higher than under a spectral neutral film [56]. In most cases, increasing the light level increases terpenoid biosynthesis, so does the concentration and the emission, which has been postulated to be due to the presence of multisubstrate and multiproduct TPSs [10,58]. For instance, after sunlight exposure there was a positive correlation between *Vitis vinifera* pinot noir linalool/nerolidol synthase 1 (VvPNLinNer1) gene expression and linalool concentration in the grape berry's mesocarp and exocarp [59]. In *Mentha piperita* leaves it was described that biosynthesis kinetics of most monoterpenoids is

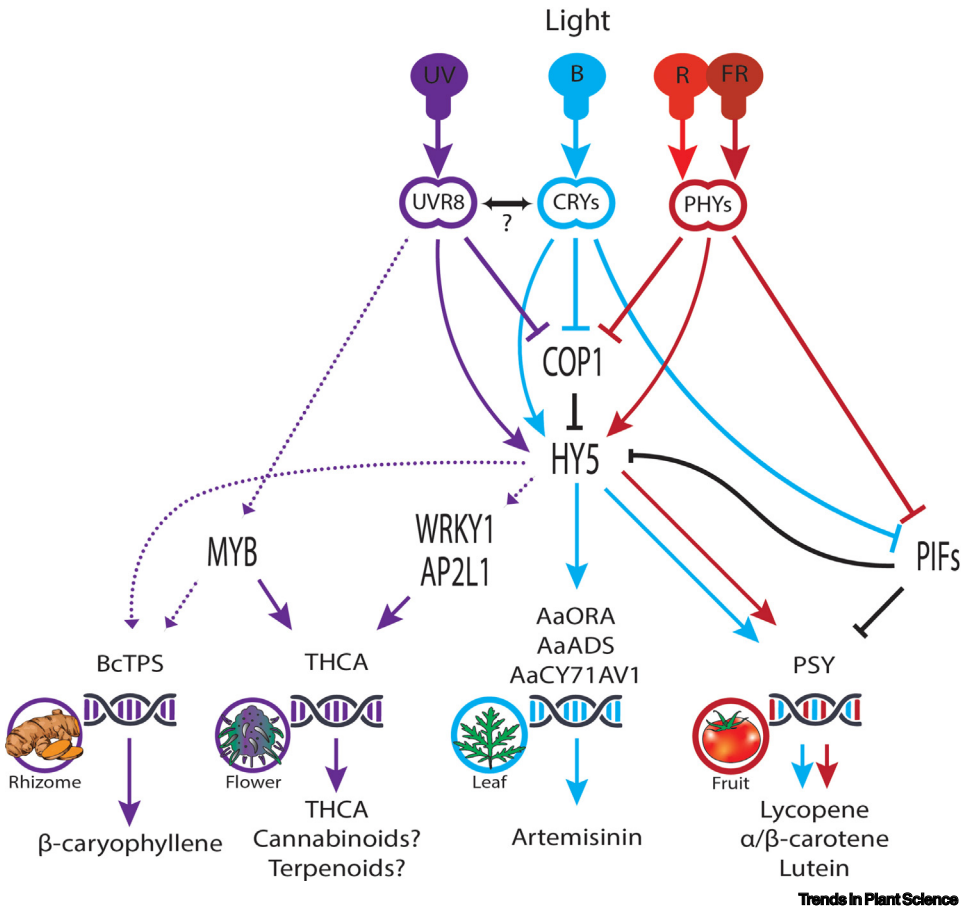

Figure 2. A simplified and hypothetical model depicting terpenoid regulation by light. The UV RESISTANCE LOCUS 8 (UVR8) signaling pathway: UVR8, cryptochrome (CRY), and phytochrome (PHY) bind CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) to prevent elongated hypocotyl 5 (HY5) inhibition. Under UV light HY5 upregulates glandular trichome-specific (WRK1) and AP2-LIKE (AP2L1) to promote the expression of tetrahydrocannabinol synthase (THCAS) which leads to the production of Δ9-tetrahydrocannabinolic acid (THCA) and potentially other cannabinoids and terpenoids in *Cannabis sativa* L flowers. UVR8 is known to interact with MYBs (MYELOBLASTOSIS), hence it is proposed that this interaction promotes the expression of *BcTPS* (β-CARYOPHYLLENE TERPENE SYNTHASE) impacting the production of β-caryophyllene in rhizomes. Under blue light, HY5 promotes the expression of genes *AaORA* (*Artemisia annua GLANDULAR TRICHOME-SPECIFIC*), *AaADS* (*A. annua AMORPHA-4,11-DIENE SYNTHASE*), and *AaCY71AV1* (*A. annua CYTOCHROME P450 MONOOXYGENASE*), consequently affecting the production of artemisinin in leaves of *Artemisia annua*. Under blue and high-ratio red:far-red (R:FR) light HY5 promotes the expression of *PSY* (PHYTOENE SYNTHASE) which regulates the production of carotenoids in tomato fruit. Under high-ratio R:FR light PHYs inhibit phytochrome-interacting factors (PIFs) which reduce *PSY* and HY5 expression. Complete arrows show the paths supported by experimental evidence while the broken arrows show hypothetical mechanisms that are compatible with current knowledge.

time-coordinated in a way that mRNA transcript accumulation of biosynthetic enzymes, enzymatic activity, and monoterpenoid content are correlated [60].

Postharvest light treatments during transportation can also prevent the loss of terpenoid-related quality in pitaya, an edible fruit from the Cactaceae family, of which the red-colored fruits are rich in PSMs with multiple health benefits (Figure 1) [61]. For instance, postharvest exposure of pitaya fruits to monochromatic B light (35 μmol/m^2/s, 2 h/day) has been positively correlated with delayed fruit senescence and increased abundances of the sesquiterpenoids α-longipinene and longifolene, while the monoterpenoid β-linalool was found to be reduced [61].

Leaves

A. annua L. is a medicinal plant highly valued for the presence of artemisinin, the sesquiterpenoid lactone with antimalarial, antitumor, and antibacterial properties (Figure 1) [46], and the discovery of artemisinin biosynthesis (by Youyou Tu, 2015 Nobel Prize in Physiology and Medicine) has led to a paradigm shift in antimalarial drug development. R and B light are both required light spectra for the regulation of terpenoid biosynthesis in *A. annua* L. The highest total content of artemisinin per plant was observed under W (R/G/B) light, followed by monochromatic B and R light, results that strongly correlate with the antimalarial activity (measure of medicinal quality) [46,62]. Generally speaking, W, monochromatic R, and B light similarly affect the relative abundance of sesquiterpenoids and monoterpenoids [62]. A proteomic analysis of *A. annua* L. leaves identified 442 terpenoid-related proteins, where 53, 20, and 31 proteins were uniquely expressed under R, W, and B light, respectively [63]. From these proteins, 53% of identified sesquiterpene, triterpene, and tetraterpene synthase genes were expressed under monochromatic R light, 58% of monoterpene, sesquiterpene and diterpene synthases genes under B light, and 55% of monoterpene, sesquiterpene, and triterpene synthases under W light [63]. Complementarily, R light resulted in the lowest content of diverse terpenoids, including monoterpenoid (camphor) sesquiterpenoids (β-caryophyllene, β-cubebene, germacrene D, and α-humulene), diterpenoid (neophytadiene), and triterpenoids (γ-sitosterol and β-amyrone), all with important and indisputable pharmacological activity [46]. However, R light can promote the production of the sesquiterpenoid, β-farnesene, and the triterpenoid, squalene in artemisia [46]. Light spectrum affects leaf anatomical structures, such as glandular trichomes which are the main machinery for terpenoid production [62]. Glandular trichome density was significantly increased under monochromatic B, G, R, and **yellow (Y) light**, compared with W light and darkness [62]. However, high-pressure sodium (HPS) plus natural light with supplemental G and UV-B light significantly increased trichome density compared with supplemental B, FR, R, and W light [64]. It is thought that optimization of artemisinin yield via increased trichome density could be achieved by manipulating light spectra; however, in the aforementioned examples there was no correlation between the content of artemisinin and increased trichome density [62,64]. Light, as opposed to darkness, can downregulate and upregulate gene expression of enzymes upstream of the mevalonate (MVA) and methylerythritol phosphate (MEP) pathways, respectively, suggesting that both pathways differ in their responses to light [65]. Moreover, light transcriptional regulation of the MEP pathway has been described in different plants (*Arabidopsis thaliana, Antirrhinum majus, A. annua L., Ginkgo biloba, Oncidium orchids*, and *Nicotiana benthamiana*), altogether highlighting that an entire set of enzymes in the upstream section is light regulated: that is, 1-deoxy-d-xyloluse 5-phosphate synthase (DXS), 1-deoxy-d-xylulose-5-phosphate-reductoisomerase (DXR), 4-hydroxy-3-methylbut-2-enyl diphosphate reductase (HDR) [66]. Light regulation of the downstream MEP pathway is critical for the biosynthesis of terpenoids required for chloroplast differentiation [67], photosynthetic and photoprotective pigments (chlorophyll and carotenoids), membrane strengthening, and oxidative protection in photosynthesis-related components such as plastoquinone, and antioxidants (isoprenoids, monoterpenoids, diterpenoids, zeaxanthin, β-carotene, tocopherol, and plastoquinone) [66,68]. The biosynthesis of artemisinin, as for all terpenoids, is divided into an upstream section (production of farnesyl pyrophosphate, FPP) and a downstream section (production of artemisinin and derivatives). The overexpression of key biosynthetic enzyme genes (DXS, DXR, HDR, and farnesyl diphosphate synthase, FPS) involved in the upstream section can result in increased levels of artemisinin, and the expression of these genes is promoted by W or B light [64]. Furthermore, the assembly of artemisinin that occurs in the downstream section is strongly dependent on the enzymes amorpha-4,11-diene synthase (ADS) and cytochrome P450 mono-oxygenase (CYP71AV1), and their gene expression is promoted by B or W light, and B, W, or R light, respectively (Figure 2) [64]. The aforementioned findings were partially confirmed by observing that B light significantly promotes the expression of ADS, but not of CYP71AV1, which correlates with significant increases in the

production of artemisinin [62]. Overexpressing *A. annua* L. cryptochrome 1 (AaCRY1) photoreceptors in four transgenic artemisia plants led to 43–62% increases in the artemisinin content compared with wild type [69]. As in tomato, B light activates AaCRYs leading to enhanced interaction with AaCOP1, and this interaction prevents the degradation of AaHY5 regulating the action of *A. annua* glandular trichome-specific AaGSW1, resulting in enhanced expression of AaORA, AaADS, and AaCY71AV1 (Figure 2) [70]. Hence, blue light must be considered as an essential spectrum in the light composition used for the enhancement of the quality of artemisia.

Ocimum basilicum L. is a culinary and medicinal herb highly valued for its flavor/aroma and health benefits derived from monoterpenoids, sesquiterpenoids, and tetraterpenoids (carotenoids) (Figure 1) [71,72]. R:B ratios ranging from 0.5 to 3 could be used to drive the production of volatile terpenoids in basil plants. A R:B ratio of 0.5 resulted in higher content of α-/β-pinene, α-/β-phellandrene, terpinolene, D-limonene, and α-bergamotene, when compared with higher R:B ratios. By contrast, a R:B ratio >1 compared with 0.5 resulted in higher content of β-cubebene and γ-muurolene, linalool, and myrcene and β-farnesene [73]. The production of monoterpenoids and sesquiterpenoids can also be affected by R and B light supplemented by different spectra (G, Y, FR, and UV light). Basil seedlings exposed for 3 weeks to a background R:B (1:1, 100 μmol/m^2/s 12 h/day) with the addition of G or Y light (50 μmol/m^2/s) induced the accumulation of monoterpenoids, while the addition of FR light (50 μmol/m^2/s) induced only the production of sesquiterpenoids [74]. Complementarily, basil plants grown under R/B/G/FR (120 μmol/m^2/s, 16 h/day) with the addition of **UV-A** (3.8 μmol/m^2/s) or UV-B (0.2 μmol/m^2/s) led to 2- and 2.5-fold increases in the amount of the monoterpenoid linalool, while **UV-C** (0.2 μmol/m^2/s) resulted in a 70% reduction of linalool [75]. Furthermore, supplemental FR light (180 μmol/m^2/s) provided to basil plants grown under R/B/G/FR (R/B/G: 150 μmol/m^2/s and FR: 2 μmol/m^2/s, 18 h/day) for either 1 or 3 weeks before harvest had no effect on the content of eugenol, eucalyptol, and linalool [76]. Moreover, increasing R light intensity negatively influenced the accumulation of the tetraterpenoids lutein and β-carotene [77]. Increased accumulation of terpenoids (linalool, germacrene-D, and, cadinol), and emission rates of volatile terpenoids (linalool, 1-8-cineole, α-bergamotene, α-guaiene, germacrene-D, (E)-β-ocimene, myrcene, and limonene) occurred under a light spectral composition of R (40–47%), B (18–20%), G–Y (40–47%), FR (8–11%), and UV-A (0.1–0.2%), compared with a light spectrum composed by R (55%), B (15%), G–Y (16%), FR (14%), and UV-A (0.1%) [78]. By contrast, the latter light spectral composition significantly reduced the concentrations of the monoterpenoid linalool (42–60%), and the sesquiterpenoids germacrene-D (35–40%) and cadinol (45–48%). Hence, a substantial increase in monoterpenoids and sesquiterpenoids is associated with an increase in the G light fraction, while it is not fully clear whether large fractions of R light (>50%) may also be associated with decreases in terpenoid levels [78]. G light has been described to reverse cryptochrome-mediated responses to B light in *A. thaliana*, but also a co-action phenomenon has been proposed between R, B, FR, and most likely G, based on the fact that CRYs and PHYs physically and functionally interact for the regulation of plant physiology and metabolism [79]. Further studies are needed to discern the effect of G light, and its potential co-action with other wavelengths and their role in the modulation of terpenoid biosynthesis.

The R:B ratio is a relevant factor when interpreting the effect of light spectra on carotenoid production. Three R:B light treatments (95:5, 91:9, and 83:17) all at 100 μmol/m^2/s, significantly increased the content of carotenoids by 37%, 42%, and 46%, respectively, compared with monochromatic R [80]. By contrast, no significant differences in carotenoid content were observed between three R:B light treatments (67:33, 50:50, and 33:67) all at 120 μmol/m^2/s [81]. However, decreased levels of the tetraterpenoid β-carotenes were observed under monochromatic R light (638 or 665 nm) and R-enriched (638 nm) R/B/FR light compared with R-enriched

(665 nm) R/B/FR light [77]. It is interesting to note that negative effects on carotenoid accumulation were observed when R light corresponded to >92% of the light spectral composition. However, comparing and concluding anything from the aforementioned studies is rather challenging due to clear differences that constrain a straightforward interpretation: light intensity of each spectrum, the R:B ratios, and the presence of FR light that differ simultaneously. Supplemental B and R light can impact terpenoid production, which can be related to spectrum but also to an increased DLI. Overall, adding R and B light seems better to significantly increase the quantity of monoterpenoids than solely using HPS lamps or natural light [72]. It is important to highlight that HPS lamps tend to increase plant temperature compared with light-emitting diode (LED) fixtures [82]. It has been suggested that high temperatures can lead to passive volatilization, as well as depletion of respiratory substrates needed for the biosynthesis of terpenoids, therefore affecting measured concentrations [83]. However, the authors ruled out the likelihood of a temperature effect on the biosynthesis and passive volatilization because in their study leaf temperature was hardly affected by light treatment [72]. A R:B ratio of 60:40 was optimal for accumulation of crucial monoterpenoids influencing basil flavor (limonene, pinene, eucalyptol, and linalool) [72]. Also, growing cycles in seasons of the year, with different light intensities and photoperiods and a natural DLI <8.62 mol/m^2/d increased the production of (S)-(–)-limonene [72]. By contrast, (R)-(+)-limonene, α-/β-pinene, linalool, and eucalyptol were increased in growing cycles where the natural DLI was >8.62 mol/m^2/d [72]. In accordance, increasing DLI from 5 to 35 mol/m^2/d linearly increased the concentrations of linalool and 1,8 cineole by fourfold [84]. The DLI correlates with substrate availability, a limiting factor in monoterpenoid biosynthesis under low light, which is linked to daily assimilation and total produced biomass [84]. Hence, increasing radiation intensity is likely enlarging the substrate pool which can be used by different terpenoid enzymes, consequently increasing (mono)terpenoid production [84]. However, high light intensities may lead to high leaf/plant temperatures, which could be counterproductive as it has been proposed that under high temperatures this substrate pool is used for growth instead of terpenoid biosynthesis [83]. The interaction between light intensity and temperature and its implications on terpenoid biosynthesis is a phenomenon that remains elusive and speculative, therefore a knowledge gap that requires further exploration. Moreover, it is important to note that more does not always mean better. In the aforementioned study, consumer preference was correlated with basil grown at 12 mol/m^2/d with the penultimate lowest concentration of monoterpenoids [84]. These results suggest that the provision of light as R:B ratios is a considerable player in light signaling influencing terpenoid production in basil.

Flowers

C. sativa L. is a medicinal plant with an important repertoire of PSMs where terpenoids, including cannabinoids, are at the top of the list providing a wide range of medicinal properties (Figure 1). Most photobiology studies in cannabis have focused on exploring the influence of light intensity and spectrum on specialized metabolites. Subcanopy lighting with R/G/B or R/B light spectra (95 µmol/m^2/s for 48 days) significantly increased the concentration of terpenoids in flower buds in the upper and lower canopy, while increases in cannabinoids were observed only in flower buds in the lower canopy [85]. Monoterpenoid abundances were primarily affected by the R/B/G spectrum provided by subcanopy lighting, while sesquiterpenoid abundances were primarily affected the intensity provided by R/G/B and R/B subcanopy lighting [85]. Moreover, there was also an intensity effect on cannabinoids abundances. Δ9-Tetrahydrocannabinol (Δ9-THC) and its precursor Δ9-tetrahydrocannabinolic acid (THCA) were significantly increased in flower buds in the lower canopy, resulting in 4% increase of total Δ9-THC under 20% higher R/G/B or R/B light compared with no subcanopy lighting [85]. Also, subcanopy lighting with R/G/B significantly increased the concentration of cannabigerolic acid (CBGA) in the top canopy flowers compared with no subcanopy lighting [85]. Additionally, a R:B ratio (4:1) top light treatment increased the concentration of CBGA, as well as cannabidiolic acid (CBDA), THCA, and cannabichromenic acid

(CBCA) compared with HPS lamps [86]. By contrast, no effect on THC and cannabidiol (CBD) concentrations was observed under an increasing B light fraction in light treatments [87]. An increasing R:FR ratio (2.83–4.04–13.49) resulted in higher levels of CBDA, β-myrcene, ocimene, and linalool, while the opposite was observed for α-pinene [88]. In *A. thaliana* R light represses PIF activity to further allow HY5 to upregulate the expression of MEP-related genes, resulting in increased monoterpenoids [89]. It has been suggested that the same happens in cannabis plants, explaining the increased levels of the aforementioned monoterpenoids. However, this does not apply to α-pinene, which could be attributed to the effect of other wavelengths in the UV-A, G, and B spectrum [88]. The latter was partially confirmed by a study reporting a decrease in the concentration of α-pinene, and β-caryophyllene under supplemental UV-A light [90]. By contrast, cannabis plants exposed to more UV-A radiation at high altitudes (1200 m above sea level) have been reported to produce higher total concentrations of terpenoids (β-caryophyllene, β-myrcene, and α-humulene) and cannabinoids (CBGA and CBCA) [91]. Supplemental UV-A in protected cultivation can increase the production of Δ9-THC in the flower by about 4%, compared with light without supplemental UV [90], albeit in other cases UV-A or UV-B, and their combination, can be negligible or detrimental to the concentration of cannabinoids and terpenoids [92–95]. Such inconsistencies may be attributed to differences in UV doses, genotypes, moment, and duration of application, and the background light intensity/spectrum. In addition, similar contrasting effects of G light on Δ9-THC have been reported, and G light seems to have an inductive effect on the accumulation of CBGA and monoterpenoids (limonene, linalool, and myrcene) [96,97].

To our knowledge, rather few studies have analyzed the light regulatory mechanism on the biosynthesis of cannabis terpenoids and cannabinoids. A proteomic analysis revealed that 40% and 66% of differentially expressed proteins in cannabis were upregulated by R and B light, respectively [98]. Moreover, a Kyoto Encyclopedia of Genes and Genomes (KEGG) functional annotation and enrichment analysis of these differentially expressed proteins unveiled that under R light, 25 proteins attributed to the metabolic pathways of limonene and pinene degradation and sesquiterpenoids and triterpenoids biosynthesis were significantly enriched [98]. As for B light, the enrichment analyses indicated that nine proteins were enriched in the carotenoids, sesquiterpenoids, and triterpenoids biosynthesis pathways [98]. In mint (*M. piperita* and *Mentha aquatica*) plants B and UV light have an effect on the transcription levels of DXS, isopentenyl-diphosphate delta-isomerase (IPPi), and geranyl diphosphate synthase (GPPS) [99,100], and these genes are well conserved in all plants, as well as in the upstream biosynthesis of cannabis terpenoids and cannabinoids [96]. The upstream section of cannabinoids synthesis depends on the MEP and polyketide pathways [96]. Compared with the MEP pathway, light regulation of the polyketide pathway is rather obscure, although it has been demonstrated that UV and B light induced mRNA accumulation of type III polyketide synthases [101]. The synthesis of CBGA is a result of the reaction between olivetolic acid (OA) and geranyl pyrophosphate (GPP), and the formation of OA depends on the action of olivetolic acid cyclase (OAC) which belongs to the type III polyketide synthases [96]. UV and B light may also have an inductive effect on OAC; however, this requires further investigation to better understand light regulation of the polyketide upstream section of cannabinoids synthesis. The biosynthesis of THCA is regulated by three trichome-specific transcription factors that modulate the expression of the THCA synthases gene (tetrahydrocannabinol synthase, THCAS), namely CsMYB1, CsAP2L1, and CsWRKY1 (Figure 2) [102]. CsAP2L1 positively regulates the transcription of THCAS, while the opposite effect is exerted by CsMYB1 and CsWRKY1 [102]. CsAP2L1 and CsWRKY1 are transcription factors belonging to the APETALA2/ethylene-response factor (AP2/ERF) and WRKY1 families, respectively [70,102]. Many of these transcription factors are B and R light regulated via HY5 [52,70]; hence, it is imperative to determine whether HY5 plays a role on the transcriptional regulation of CsAP2L1 and CsWKR1 under B or R light, determining the biosynthesis of terpenoids

and cannabinoids in cannabis trichomes (Figure 2). Furthermore, UV light may also have an intrinsic role in the regulation of terpenoid biosynthesis in cannabis via UVR8 and HY5. UV light activates UVR8 which can interact with MYB transcription factors regulating growth and development [103]. UVR8 potentially interacts with CsMYB1, thus regulating the biosynthesis of cannabinoids (Figure 2). Similarly, UVR8 signaling can upregulate the transcriptional induction of HY5 promoting the function of CsAP2L1 and CsWRKY1, hence forming a potential regulatory mechanism in the production of cannabinoids (Figure 2) [103]. However, how these interactive mechanisms act specifically in cannabis has yet to be established.

Light intensity may also influence terpenoid yield as a consequence of greater flower yields. Increasing light intensity from 200 to 1800 μmol/m^2/s linearly increased flower yield, which led to an increase in the total cannabinoid yield (g/m^2), total terpenoids, myrcene, and limonene content (mg/g^1 of flower), respectively [92]. Similarly, cannabis plants grown under three light intensities (600, 800, and 1000 μmol/m^2/s) showed increased flower, cannabinoids, and terpenoids yields [104]. Also, photoperiod can influence the production of cannabinoids in cannabis. In one genotype a dynamic photoperiod extended from 12 h to 14 h or shortened from 14 h to 12 h and 10 h increased CBD yield compared with a static 12 h photoperiod, while in another genotype shortening it from 14 h to 12 h increased Δ9-THC yield [105]. In industrial hemp, a photoperiod exceeding 13 h and 40 min during the growing season resulted in the highest leaf and floral yields [106]. When the photoperiod is extended, flower biomass and cannabinoid content are positively influenced, while when it is shortened, only the flower biomass was affected [105]. In *Glycine max* L., extending the photoperiod delayed reproductive development, and increased cumulative intercepted radiation and biomass production, resulting in more assimilates partitioned to reproductive organs [107]. In cannabis, delayed reproductive development could potentially give more time for radiation interception, benefiting flower biomass production thus increasing the production and accumulation of specialized metabolites in the flower, but such assumptions can still not be easily demonstrated. Speculations on carbohydrate dynamics suggest that under extended photoperiod conditions the extra light provided to the plant may lead to starch storage in roots and stems, which could be remobilized to glandular trichomes for the biosynthesis of terpenoids [105]. It is known that increases in the partition of the assimilates towards starch accumulation is strongly dependent on photoperiod and not so much on light intensity [108]. Also, under long-term abiotic stress, mint plants can remobilize starch to favor the production of monoterpenoids for the protection of plant tissue [108]. Any extra provision of light may represent a source of photo-oxidative stress via production of reactive oxygen species (ROS) which affect cellular and photosynthetic components in the plant [109]. To mitigate ROS damage, plants produce endogenous isoprenoids, monoterpenoids, and sesquiterpenoids acting as antioxidants, hence posing one explanation for the increased terpenoid yields under extended photoperiods [110]. Cannabis has been described to be particularly different from other crops because of its ability to cope with considerably high light intensities (≈1800 μmol/m^2/s) [92]. Under excessive amounts of light, carotenoids can protect the photosynthetic machinery from photo-oxidative damage, and carotenoids are also connected to chloroplast development [111]. Furthermore, in *N. benthamiana* and *A. thaliana* plants, isoprene emission was positively associated with chlorophyll (*a* and *b*), carotenoid, and xanthophyll content, which has been associated with feedback regulation of gene expression from the MEP pathway [112]. Also, under high and fluctuating light stress, isoprene upregulated the expression of genes involved in chloroplast development and chlorophyll synthesis, photoprotection and stabilization of photosystems I and II, and production of unsaturated fatty acids and thylakoid membrane proteins [112]. In consequence, isoprene can improve photochemical efficiency, membrane stability, and minimize chloroplast damage [112]. The synthesis of isoprene depends on the production of pyruvate and glyceraldehyde 3-phosphate which are derived from the Calvin cycle; therefore, the production of isoprene is directly dependent on

photosynthesis and light is a driver in these processes. Altogether this suggests that the production of one terpenoid, and perhaps others, may be critical for plants to cope with abiotic stress such as high light intensity. Analysis of the biogenic volatile organic compounds shows that cannabis plants produce isoprene [113]; however, no studies have evaluated whether isoprene aids in coping with high light intensities. To the best of our knowledge, there are various undetermined phenomena regarding cannabis assimilates dynamics, oxidative stress and its implications in the photosynthetic machinery, PSM profiles and contents, and their regulatory mechanisms. Therefore, we need to understand the means by which cannabis plants cope with excess photon energy, as well as the dynamics between fixated carbon into structural and non-structural carbohydrates, and PSMs (aiding in photoprotection and electron scavenging) to better explain trichome and terpenoid biosynthesis productivity under specific light conditions in cannabis and other plants.

Conflicting results on the unclear trends regarding the effect of light on terpenoids in cannabis, and other medicinal plants, call for a deeper analysis of the underlying mechanism regulated by light. Prospective studies should focus on correlating gene expression of specific terpenoids and cannabinoids biosynthetic enzymes, corresponding enzymatic activity, and final concentration under comparable experimental light conditions. Special attention should be given to enzymes known to be light-influenced, and those belonging to the downstream section of the biosynthesis of terpenoids and cannabinoids.

Rhizomes

Light regulation of terpenoid biosynthesis also occurs in underground organs. Light is intercepted mostly, if not entirely, by leaves, while also influencing underground organs. *Curcuma* spp. is a plant belonging to the family Zingiberaceae; its rhizome contains a vast repertoire of both medicinal and nutritional compounds, including terpenoids (Figure 1) [47]. Exposing curcuma plants to elevated UV-B light (ambient ± 9.6 kJ m/2d) promoted the production and diversity of sesquiterpenoids and the reduction of most monoterpenoids, except for 1,8-cineole, in the rhizome [114]. The terpenoids γ-amorphene, β-caryophyllene, furanodiene, β-progesterone, pulegone oxide, retroprogesterone, and verrucarol were detected only under elevated UV-B [114]. Furthermore, elevated UV-B promoted the production of the anticancerous sesquiterpenoids α-terpinolene, β-caryophyllene, β-sesquiphellandrene, and curzerene, which were significantly increased by 61%, 60%, 32%, and 10%, respectively, compared with no elevated UV-B [47,114]. Ginger (*Zinger officinale*) is another rhizomatous plant from the family Zingiberaceae with nutritional and medicinal properties derived from terpenoids and other compounds [115]. Green-enriched sunlight increased the content of eight monoterpenoids by 16–40%, while sesquiterpenoids were both positively (3–92% increase) and negatively (2–9% decrease) affected compared with unenriched sunlight [115]. UV-B may also be used to regulate the production of the oleanane-type triterpenoid saponin glycyrrhizin (anticancerous and antiviral) in *Glycyrrhiza uralensis* rhizoids (Figure 1). Exposure of 3-month-old plants for 15 and 3 days to low and high UV-B intensity (0.43 and 1.13 W/m^2) significantly increased the concentration of glycyrrhizin by 25% and 16%, respectively [115]. Light spectrum can influence the exudates, including terpenoid-derived compounds, of belowground organs such as rhizomes; however, it is not fully known how light spectra perceived by leaves affect belowground organs [116]. CRYs, PHYs, and UVR8 are also present in underground organs to directly sense light, a situation that occurs only when the roots are within the first 10 mm of the soil/substrate or *in vitro* studies [117]. The presence of photoreceptors in the roots may play a regulatory role connected to light signaling components coming from aboveground. HY5 is a mobile molecule involved in light signaling from shoot to root, and is therefore a key integrator of light regulation of PSM biosynthesis in underground organs [118]. Under UV-B exposure HY5 transcriptional induction can occur via UVR8 signaling, consequently regulating the transcription of other genes involved in terpenoid biosynthesis (Figure 2) [103]. Little is known about terpenoid-related light transcriptional regulation in underground organs;

however, an increasing number of uncharacterized MYBs have been described in the roots, which might play a role in the underground stress response, including exudation of terpenoids, in various plants [119]. For instance, MYBs are involved in aboveground transcriptional regulation of β-caryophyllene TPS in the orchid *Dendrobium officinale* (*DoβcarTPS*) [120]. βcarTPSs have a conserved evolutionary association with the production of sesquiterpenoids in different plants [120]. Because MYBs have been described to interact with UVR8 to regulate the expression of terpenoids [103], it could be suggested that under UV MYB and UVR8 interact to promote the expression of βcarTPS, consequently impacting the biosynthesis of β-caryophyllene in ginger and curcuma rhizomes (Figure 2). Different TPSs in ginger and curcuma have been described [121], but their regulatory mechanism correlating light, gene expression, and terpenoid content have not been established.

Concluding remarks and future perspectives

Spectral composition (the various wavelengths) is the most important light component to extensively modify chemical diversity of terpenoids in leaves, flowers, fruits, and rhizomes, while light intensity and photoperiod pose an opportunity to mainly impact abundance. Little attention has been given to understanding the effect of light intensity and photoperiod on the molecular mechanisms determining the occurrence and abundance of plant terpenoids. Both light intensity and photoperiod are important light features because they represent the amount of energy the plant can get to fixate carbon that will be directly or indirectly used for growth and biosynthesis of terpenoids and other specialized metabolites. At the same time, such energy can also represent a source of stress in the form of ROS, which the plant can counteract by producing specific terpenoids. Based on recent studies in basil and cannabis we can state that increases in terpenoid production caused by more assimilates allocated towards biomass and specialized metabolism tend to be linearly correlated with increasing light intensity and photoperiod [84,92,105]. However, our understanding of how assimilates are mobilized or remobilized under specific light environments remains elusive. Moreover, what happens with the allocation of assimilates under oxidative stress is also insufficiently understood. Henceforth, special attention should be given to the study of carbohydrate dynamics, photoprotection, and the antioxidant activity of terpenoids.

UV triggers a signaling pathway involving key elements such as UVR8, HY5, and COP1, while the signaling pathway for UV-A is also modulated via CRYs [19]. The detailed picture of UV signaling remains unclear and underexplored, with implications for our knowledge of terpenoid biosynthesis. UV and B light responses have been proposed to trigger a potential interaction between UVR8 and CRYs, but the underlying processes on terpenoid regulation are rather obscure. Further research is required to elucidate the mechanism behind UV regulation on terpenoids and its potential interaction with blue light responses.

R and B are mutually dependent spectra, as they both trigger the light signaling that regulates the biosynthesis of various terpenoids, in which the transcription factor HY5 has a central role. The effect of R:B ratios cannot be easily compared and interpreted, thus hindering straightforward conclusions. Factors including DLI, photoperiod, light intensity, supplemental spectra, and differences in R:B ratios represent unavoidable sources of variation. This variation is likely determining the effect that light may have on plant terpenoids. Based on the reviewed studies, the presence and fraction of R, B, and G in the light spectrum matters, highlighting that decreases in tetraterpenoids, and increases in monoterpenoid and sesquiterpenoid concentrations, were mostly associated with a R light fraction of >50% of the instantaneous photon flux. Moreover, an increase in monoterpenoids and sesquiterpenoids seems to be associated with a G fraction of >40% compared with a lower or no fraction of G.

Another important aspect of steering terpenoid production is to match consumer acceptance (quality) with plant phenotype (terpenoids). Most studies do not consider any correlation of

Outstanding questions

What is the role of different R:B ratios in determining the interaction between CRYs and PHYs, and how does such interaction affect light regulation of terpenoids?

To be or not to be proper. What is the proper and comparable experimental design to study the effect of R and B light? For instance, if we change the fraction of R light, by default other light spectra will change as well, and if we add more R light then light intensity will increase.

Does every nanometer count? Are UVR8, CRY, and PHY responses the same for every single wavelength within the UV, B, and R spectra, respectively?

Is there any crosstalk between UVR8 and CRYs determining light regulation of terpenoids? Is this crosstalk similar among species and their organs?

Is the effect of light intensity, photoperiod, and DLI on terpenoids a plant response to mitigate photo-oxidative stress and photo-inhibition, therefore influencing terpenoid biosynthesis? Does this effect apply to both above- and belowground organs?

How much of the photon energy is transduced into structural and non-structural carbohydrates, and terpenoid biosynthesis? And what proportion of the non-structural carbohydrates is used for terpenoid biosynthesis?

What is the light cue (spectrum, intensity, or photoperiod) required by the plant to initiate carbon reallocation from the stored carbon to the site where terpenoids are being produced?

terpenoid abundances and profiles with consumer acceptance. Therefore, prospective research must also include studies that define, test, and establish the quality of plant produce [84]. Globally speaking, the aforementioned recent developments show a promising future application modifying the light environment to steer terpenoid production and consequently improve the quality of plants (Figure 2) (see Outstanding questions).

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Declaration of interests

No interests are declared.

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