

Review

# Current Context of *Cannabis sativa* Cultivation and Parameters Influencing Its Development

Andreia Saragoça <sup>1</sup>, Ana Cláudia Silva <sup>2</sup>, Carla M. R. Varanda <sup>3,4</sup> , Patrick Materatski <sup>3</sup> , Alfonso Ortega <sup>5,6</sup>, Ana Isabel Cordeiro <sup>1,3</sup> and José Telo da Gama <sup>1,7,\*</sup> 

<sup>1</sup> Biosciences School of Elvas, Polytechnic Institute of Portalegre, 7350-092 Elvas, Portugal; 18954@ippportalegre.pt (A.S.); ana\_cordeiro@ippportalegre.pt (A.I.C.)

<sup>2</sup> Companhia Extremeña de Investigación y Producción Agroalimentaria S.A., Ctra. Villafranco-Balboa 1.3, 06195 Badajoz, Spain; anasilva3089@gmail.com

<sup>3</sup> Universidade de Évora, MED—Mediterranean Institute for Agriculture, Environment and Development & CHANGE—Global Change and Sustainability Institute, Largo dos Colegiais 2, 7004-516 Évora, Portugal; carla.varanda@esa.ipsantarem.pt (C.M.R.V.); pmateratski@uevora.pt (P.M.)

<sup>4</sup> Research Centre for Natural Resources, Environment and Society (CERNAS), School of Agriculture, Santarém Polytechnic University, Quinta do Galinheiro-S. Pedro, 2001-904 Santarém, Portugal

<sup>5</sup> Research Group FBCMP, UEx, Facultad de Ciencias, Universidad de Extremadura, 06008 Badajoz Extremadura, Spain; aortegagarrido@unex.es

<sup>6</sup> Instituto Universitario de Investigación de Recursos Agrarios (INURA), Universidad de Extremadura, Avda. de la Investigación s/n, Campus Universitario, 06006 Badajoz, Spain

<sup>7</sup> VALORIZA—Centro de Investigaçao para a Valorizaçao de Recursos Endógenos, 7300-110 Portalegre, Portugal

\* Correspondence: jose.gama@ippportalegre.pt

## Abstract

*Cannabis sativa* L. is a versatile plant with significant medicinal, industrial, and recreational applications. Its therapeutic potential is attributed to cannabinoids like THC and CBD, whose production is influenced by environmental factors, such as radiation, temperature, and humidity. Radiation, for instance, is essential for photosynthetic processes, acting as both a primary energy source and a regulator of plant growth and development. This review covers key factors affecting *C. sativa* cultivation, including photoperiod, light spectrum, cultivation methods, environmental controls, and plant growth regulators. It highlights how these elements influence flowering, biomass, and cannabinoid production across different growing systems, offering insights for optimizing both medicinal and industrial cannabis cultivation. Studies indicate that photoperiod sensitivity varies among cultivars, with some achieving optimal flowering and cannabinoid production under extended light periods rather than the traditional 12/12 h cycle. Light spectrum adjustments, especially red, far-red, and blue wavelengths, significantly impact photosynthesis, plant morphology, and secondary metabolite accumulation. Advances in LED technology allow precise spectral control, enhancing energy efficiency and cannabinoid profiles compared to conventional lighting. The photoperiod plays a vital role in the cultivation of *C. sativa* spp., directly impacting the plant's developmental cycle, biomass production, and the concentration of cannabinoids and terpenes. The response to photoperiod varies among different cannabis cultivars, as demonstrated in studies comparing cultivars of diverse genetic origins. On the other hand, indoor or in vitro cultivation may serve as an excellent alternative for plant breeding programs in *C. sativa*, given the substantial inter-cultivar variability that hinders the fixation of desirable traits.

**Keywords:** canabinoide synthesis; cannabis flowering; indoor cultivation; light spectrum; plant development; plant hormones; plant physiology; photoperiod effects



Academic Editor: Paulo Mazzafera

Received: 19 May 2025

Revised: 21 July 2025

Accepted: 23 July 2025

Published: 29 July 2025

**Citation:** Saragoça, A.; Silva, A.C.; Varanda, C.M.R.; Materatski, P.; Ortega, A.; Cordeiro, A.I.; Telo da Gama, J. Current Context of *Cannabis sativa* Cultivation and Parameters Influencing Its Development. *Agriculture* **2025**, *15*, 1635. <https://doi.org/10.3390/agriculture15151635>

*Agriculture* **2025**, *15*, 1635.

<https://doi.org/10.3390/agriculture15151635>

**Copyright:** © 2025 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

## 1. Introduction

Plants of the genus *Cannabis* are annual herbaceous plants that belong to the family Cannabaceae [1]. *Cannabis (C.) sativa* Linnaeus (L.) was first classified in 1753 by Linnaeus in *Species Plantarum* [2]. Later, two other species were also described, *Cannabis indica* Lam. and *Cannabis ruderalis* Janisch [2,3]. However, many authors recognize only *C. sativa* as a species and the others as subspecies [4]. Subspecies groups include *C. sativa* subsp. *sativa*, *C. sativa* subsp. *indica*, *C. sativa* subsp. *ruderalis*, *C. sativa* subsp. *Spontanea*, and *C. sativa* subsp. *Kafiristanca* [5,6].

There are both dioecious and monoecious varieties, and morphologically, the plant exhibits a straight stem that can reach up to 4 m in height, is slightly lignified, and bears palmate leaves and small flowers grouped into dense inflorescences [7]. Cultivation of this species has been documented for over 6000 years in East Asia [8]. It is a crop with a remarkably high growth rate, capable of producing up to 250% more fiber than cotton on the same land area. Additional advantages include its minimal requirement for herbicides, its role in enriching soil nutrients, and its potential to improve air quality [9]. From a nutritional standpoint, the crop does require an adequate concentration of nitrogen, potassium, and phosphorus. At low concentrations of these elements, the plants tend to develop inflorescences with a high cannabinoid content [10–12]. However, when nitrogen levels are high, the concentration of these compounds declines [10].

Furthermore, the plant is able to synthesize secondary metabolites with therapeutic potential, which are classified into two main groups: cannabinoids and non-cannabinoids. Cannabinoids are characterized by a 21-carbon terpenophenolic structure [13]. This group includes compounds such as tetrahydrocannabinol (THC) and cannabidiol (CBD) [14]. The non-cannabinoid group consists of phenolic compounds such as flavonoids, as well as terpenes and alkaloids. These compounds are responsible for the plant's color, aroma, and defense mechanisms and are of interest due to their potential use as flavoring agents, anti-inflammatory, antipyretic, or anticancer compounds [15,16].

This review aims to contextualize current cannabis cultivation, exploring its present-day applications, the most suitable cultivation types depending on the intended final product, and how it is strongly influenced by factors such as radiation, light spectrum, photoperiod, and the use of phytohormones. Gaining a deeper understanding of these parameters may be crucial for developing advanced plant improvement strategies and obtaining uniform, high-yielding, and more productive cultivars.

## 2. Biology and Applications of *C. sativa*

*Cannabis* is one of the earliest domesticated species, recognized for its wide range of applications in medicine, cosmetics, and recreation. However, its recreational use has sparked considerable debate, as it remains prohibited in many countries. One of the earliest records of its medicinal application dates back to 2700 BCE, when Emperor Shen-Nung documented cannabis in the first Chinese pharmacopoeia as a treatment for malaria, rheumatic pain, and menstrual disorders [17]. Since then, cannabis-derived products have been used to manage a wide range of medical conditions such as chronic pain, muscle spasms, chemotherapy-induced nausea, appetite loss in HIV patients, sleep disorders, Tourette's syndrome, anorexia, arthritis, glaucoma, and inflammatory bowel disease [18–24]. Medicinal cannabis products are primarily derived from the plant's dried flowers, extracts, or oils, which contain a wide array of active compounds. The cannabis plant can synthesize over 500 s metabolites, including more than 180 known cannabinoids out of the 1600+ chemical compounds identified in *C. sativa* spp. [25–27]. These therapeutic effects are primarily due to cannabinoids, a class of compounds found in cannabis, and may be enhanced by other bioactive components, particularly terpenes, which are suggested to

have positive effects in oncology patients [25,26]. The legalization of cannabis for medicinal use in various nations has led to increased global production in recent decades [25].

Cannabinoids are known to interact with the endocannabinoid system (ECS) in the gastrointestinal tract, indicating potential anticarcinogenic effects in colorectal cancer (CRC) through anti-proliferative, anti-inflammatory, and apoptotic mechanisms. Although more research is needed to understand the effects of *C. sativa* on CRC [18–24]. Among cannabinoids, THC was the first psychoactive compound isolated in 1942, followed by the isolation of cannabidiolic acid (CBDA) in pure form by Krejčí and Šantavý in 1955 [28], and these compounds are the most relevant and abundant [26,27]. The three subspecies—*C. sativa* subsp. *sativa*, *C. sativa* subsp. *indica*, and *C. sativa* subsp. *ruderalis*—are known to produce the highest concentrations of psychotropic secondary metabolites, mainly subsp. *sativa*.

In 2020, global legal sales of high-THC cannabis reached USD 23.7 billion, largely driven by markets in the USA and Canada. Sales are expected to surpass USD 60 billion by 2027, bolstered by ongoing legalization and market expansion across Europe, Latin America, and parts of Asia [29,30]. For all this, it is necessary to optimize production systems for developing products with specific cannabinoid and terpene profiles [31] and to delve deeper into the interactions between cannabinoids and other plant components, such as terpenes and flavonoids may enhance their medicinal properties [25].

On the other hand, there is industrial hemp, which is increasingly gaining significance in the market due to the wide variety of by-products obtained from it. From the cultivars intended for this purpose, by-products are primarily obtained from the stems, comprising approximately 85% pulp used for biofuels and 15% fiber suitable for the textile, construction, and paper industries [32]. The leaves and flowers are utilized in the cosmetic and chemical industries due to their high content of antioxidants, insecticidal, and volatile compounds such as monoterpenes, sesquiterpenes, or terpenoids, which can be separated by distillation to produce essential oils [33]. Finally, the seeds possess significant nutraceutical potential due to their content of easily assimilable fats and proteins with antioxidant capacity, along with other bioactive components that confer value as additives or supplements in the food industry, although the seeds can also be refined into oil and employed in the production of lotions and other cosmetic products [34]. Like the medicinal cannabis sector, the industrial hemp market is undergoing continuous growth due to its versatility and adaptability to emerging applications [35]. In 2021, it reached a value of USD 4.13 billion, with a projected annual growth rate of 16.8% between 2022 and 2030 [36]. According to various sources, this growth is being realized, as global market estimates indicate a value of USD 5.49 billion in 2023. Among the leading producers of industrial hemp are Canada, China, and the European Union [37].

Other potential uses of cannabis include applications in the agricultural sector and as a remediation agent. Various studies emphasize that cannabis is well-suited for crop rotation with cereals and legumes, particularly to produce oilseeds or fiber [38,39]. This is largely due to hemp's ability to rapidly cover the soil surface, outcompeting weeds, and its capacity to suppress pathogenic fungi such as *Verticillium dahliae* and phytopathogenic nematodes such as *Meloidogyne chitwoodi* and *Meloidogyne hapla*. For these reasons, its incorporation into cropping systems may contribute to improved soil conditions [40,41].

Its potential use as a phytoremediator of xenobiotic compounds has been known since 1998, when hemp was grown in the Chernobyl “exclusion zone” following the 1986 nuclear power plant accident [42] to determine whether it could remove harmful compounds from the soil [42], yet the results were never published in a peer-reviewed scientific journal. The main characteristic that makes this species particularly suitable for remediation is its deep root system, which can reach considerable depths and is capable of absorbing contaminants dissolved in the lower soil layers [43].

Another ecological function of cannabis is its ability to mitigate the greenhouse effect through two main mechanisms: carbon sequestration and the attenuation of methane emissions. *C. sativa* plants are carbon-neutral or even carbon-negative, depending on the cultivation practices employed, and can capture and store up to 22 metric tons of carbon dioxide (CO<sub>2</sub>) per hectare [39]. In addition, biochar produced from cannabis plants has been shown to reduce methane diffusion [44].

Although there are phenotypic similarities between cultivars cultivated for different purposes, morphological and physiological distinctions can be observed [45]. Cultivars intended for the pharmaceutical industry tend to be smaller in size, with a bushier appearance and numerous stem branches, abundant leaves, and inflorescences. Primarily, only female-flowering plants are utilized, as they possess a high density of glandular trichomes, which synthesize substantial quantities of secondary metabolites and cannabinoids [46,47]. In contrast, cultivars cultivated for other industrial applications prioritize vegetative development; they are generally taller, exhibit a more tree-like structure with fewer stems, a high leaf density, and finer leaves [46].

### 3. Influence of Light Quality, Intensity, and Photoperiod on *C. sativa* Cultivation

The development of *C. sativa*, including the biosynthesis and accumulation of cannabinoids and terpenes, is primarily governed by the plant's genotype, although environmental conditions exert a substantial modulatory effect [48]. A range of abiotic factors—such as photoperiod [49], temperature, light intensity [50], light spectrum [51–53], nutrient availability [10], irrigation regimes, and drought stress [54,55], as well as pruning techniques [56]—have been shown to significantly influence plant performance and yield. Notably, a large proportion of recent studies have focused on the effects of light, due to its central regulatory role in plant physiology.

Light radiation modulates several key physiological and developmental processes, including the synthesis of photosynthetic pigments (e.g., chlorophyll and carotenoids), photosynthetic efficiency, vegetative-to-reproductive phase transitions, stem elongation, stomatal conductance, leaf expansion, and secondary metabolism [57]. Among the properties of light, intensity, spectral composition (wavelength,  $\lambda$ ), and photoperiod are of particular importance [58–62].

The photosynthetically active radiation (PAR) spectrum utilized by plants spans wavelengths from approximately 400 nm (blue light) to 750–800 nm (far-red (FR) light) [63], directly affecting photosynthetic capacity and, consequently, crop productivity [64]. These wavelengths are perceived by specialized photoreceptors. Phytochromes, for example, switch to their biologically active form under red light and revert to an inactive state in response to far-red light. Other key photoreceptors include cryptochromes and phototropins, which are sensitive to blue and ultraviolet-A (UV-A) radiation [65]. While phytochromes and cryptochromes co-regulate crucial developmental processes, such as seed germination, photomorphogenesis, floral induction, and circadian rhythms [66,67], phototropins are primarily involved in phototropism, stomatal opening, chloroplast relocation, and leaf positioning [68,69].

Suboptimal light environments—in terms of spectral quality, intensity, or photoperiod—can impair plant development and delay growth. Such limitations negatively impact processes such as photosynthesis, particularly the efficiency of the electron transport chain during the photochemical phase [70]. Under low-light conditions, *C. sativa* exhibits reduced foliar development, diminished inflorescence size, and directional growth oriented towards available light sources [71]. Furthermore, light deficiency may induce the accumulation of reactive oxygen species (ROS), which, at elevated levels, can lead to oxidative stress and

lipid peroxidation of cellular membranes, although these phenomena can also occur due to excessive radiation [72]. Despite these stressors, cannabis plants possess acclimatory mechanisms that enable them to modulate photosynthetic performance in response to changing environmental conditions [73].

Over the past five years, an increasing number of studies have examined the impact of specific wavelengths and photoperiod regimes on *C. sativa*, with particular attention to their effects on plant growth, developmental transitions, and cannabinoid biosynthesis.

Changes in the quantity and quality of light influence the photosynthetic performance of plants, eventually causing alterations in growth [74]. A broad and balanced light spectrum, with an appropriate ratio of blue to red light, is essential for optimizing both plant performance and overall health, as it influences key physiological parameters such as the photosynthetic rate [75,76], light use efficiency (LUE) [76,77], leaf area [76], foliar chlorophyll content [78], and the distribution of dry mass across different plant organs [79].

The red-to-blue light ratio also plays a critical role in morphogenesis. For example, in species such as *Chrysanthemum morifolium*, *Lavandula dentata*, and *Rosa canina*, reduced red/far-red (R:FR) light ratios have been associated with improved rooting success in vegetative cuttings [63,80–82]. Therefore, the targeted manipulation of light spectra represents a viable strategy to modulate plant morphology, metabolic activity, and flowering patterns [83].

Under light competition caused by canopy shading, neighboring plants preferentially absorb red and blue wavelengths through chlorophyll, while far-red light is mostly reflected or transmitted. This results in a decreased R:FR ratio, which activates a suite of shade-avoidance responses such as stem elongation, leaf expansion, and altered flowering dynamics [84]. In parallel, increasing light intensity—typically expressed as photosynthetic photon flux density (PPFD)—has been associated with greater inflorescence biomass, among other outcomes [85–87]. Conversely, high PPFD combined with a spectrum low in white light can overexcite the photosystems, potentially causing bleaching of the inflorescences. This phenomenon is likely related to the overproduction of ROS. Interestingly, bleached inflorescences often exhibit higher total cannabinoid concentrations, mainly due to elevated levels of CBD, possibly because cannabinoids function as potent antioxidants [88,89].

In *C. sativa* cultivation, various spectral compositions and light intensities have been tested to assess their impact on vegetative growth, inflorescence development, floral initiation and duration, and the biosynthesis and accumulation of secondary metabolites. Optimizing specific wavelengths ( $\lambda$ ) in *C. sativa* spp. represents a major challenge in enhancing both yield and quality (Table 1), primarily by improving photosynthetic performance, dry matter production, and overall crop output [49,90,91].

**Table 1.** Effects of different light spectra on *C. sativa* physiology and cannabinoid production.

Light Parameter	Effect on Growth	Effect on Cannabinoid/Terpene Synthesis	References
Blue Light (400–500 nm)	Promotes compact growth, leaf expansion	Increases THC and CBD content	[51,92–94]
Red Light (600–700 nm)	Enhances stem elongation, flowering	Modulates flowering time, may affect cannabinoids	[75,76,95,96]
Far-Red Light (700–750 nm)	Influences flowering and shade avoidance	Alters secondary metabolite profiles	[63,84,97–99]
Light Intensity	Higher intensity increases photosynthesis	Enhances biomass and cannabinoid yield	[85–89,95,96,100,101]
Photoperiod	Controls flowering induction	Affects timing and levels of cannabinoid accumulation	[41,49,99,102]

However, findings across studies have often been inconsistent and genotype-dependent [58,63,103–107]. This variability extends beyond cannabinoid biosynthesis. For example, Danziger & Bernstein [63] and Reichel et al. [52] demonstrated that the time required for plants to reach maximum height also varies with genotype. Consequently, it remains challenging to establish a universal spectral treatment regime for the pre-flowering or early-flowering phases aimed at controlling plant height.

Regarding the influence of blue and ultraviolet (UV) light on the cultivation of cannabis cultivars, increased intensity within this spectral range has been shown to significantly reduce the dry weight of inflorescences [53,86], although it does not appear to affect photosynthesis, stomatal conductance, or transpiration rates in most of the evaluated genotypes [92]. In Carranza-Ramírez et al. [93], the application of blue light to three medicinal cannabis cultivars (Calotweed, Highcol, and Souce Cauca) significantly enhanced growth, increasing fresh shoot biomass by 15.1% and dry biomass by 27% compared to white light. This was likely due to improved net photosynthesis, greater stomatal conductance and transpiration, along with reduced oxidative stress.

With respect to cannabinoid synthesis and content, short-wavelength radiation (i.e., blue and UV light) increased the concentrations of all cannabinoids measured in the study by Magagnini et al. [51] and enhanced THC levels in two of the three genotypes analyzed by Jenkins & Livesay [92]. Conversely, Rodriguez-Morrison et al. [53] reported either a decrease or no effect on cannabinoid concentrations following UV exposure, depending on the genotype studied. Furthermore, excessive exposure to this spectral range may compromise green leaf performance [108,109] and reduce inflorescence dry mass [110,111].

Kotiranta et al. [94] found that the absence of light in this range did not significantly increase stem size nor did the application of blue and UV light significantly enhance secondary metabolite accumulation in the inflorescences or negatively impact inflorescence yield. However, a slight increase in cannabinoid and terpene content was observed [94].

In *C. sativa*, dry matter allocation among leaves, stems, and roots can be modulated by the red to far-red (R:FR) light ratio [112]. This phenotypic plasticity presents an opportunity to optimize cultivation strategies by tailoring the light spectrum to favor specific developmental outcomes, such as enhanced inflorescence biomass or targeted vegetative growth, depending on the intended use of the crop [79,113,114].

Recent studies indicate that increasing far-red (FR) light can enhance the photosynthetic rate in certain *C. sativa* genotypes, though this does not necessarily translate into higher floral yield. Danziger and Bernstein [63] observed that although some genotypes exhibited increased photosynthetic activity under a reduced R:FR ratio, this response did not correlate with an increase in inflorescence biomass. This finding suggests that photosynthetic rate alone is not a reliable indicator of lighting efficacy in *C. sativa*. A similar conclusion was supported by Zhen and Bugbee [97], who showed that substituting 10–40% of PAR with FR light did not significantly alter the photosynthetic rate across 14 different species. Collectively, these results indicate that manipulation of the R:FR ratio should be approached with caution and tailored to specific cultivation goals—for instance, prioritizing the accumulation of secondary metabolites rather than generic photosynthetic indicators.

The results of Holweg et al. [95] demonstrate that white light enriched with dual red peaks (640 and 660 nm) significantly increases inflorescence weight and total biomass production in *C. sativa*, compared to light containing only a single 660 nm peak—regardless of light intensity (PPFD). This response appears to be associated with the overlap between the absorption peaks of chlorophyll a and b, which enhances photosynthetic efficiency [100,101]. The appropriate spectral combination proved particularly effective under lower light intensities, suggesting that spectral tuning can compensate for energy limitations. Additionally, the exclusive use of 660 nm light may inhibit flowering in short-

day plants [96], potentially explaining the reduced floral biomass under such conditions. Increased plant height under certain spectra also appears to benefit canopy architecture, promoting better light penetration and greater dry matter production [101,115,116]. These findings highlight the importance of integrating spectral composition and light intensity to optimize floral yield and metabolic quality in medicinal *C. sativa* cultivars.

An alternative strategy involves applying pulses of R or FR light at critical stages of vegetative development to enhance cannabinoid content. For instance, FR could be applied at the onset of flowering to stimulate elongation and increase plant volume and then withdrawn during the final flowering stages to prevent reductions in secondary metabolite concentrations. This approach may also contribute to energy savings, as FR supplementation would only be used strategically to adjust the R:FR ratio when required.

In Kotiranta et al. [98], when working with the industrial hemp cultivar “FINOLA”, evidence was provided that modulating the R:FR ratio during the flowering period can serve as a tool to influence plant morphology. This included the activation of genes involved in auxin biosynthesis and cell elongation [117], enhanced light use efficiency (LUE), and altered floral cannabinoid and terpene profiles. In Peterswald et al. [99], therapeutic cultivars such as Hindu Kush, Northern Lights (both high-THC), and *Cannatonic* (high-CBD) were studied. Although FR treatment did not significantly impact floral biomass yield, the findings emphasized the critical role of genotype. The study also highlighted that 4 h FR treatments under a 12 h photoperiod reduced biomass yield, whereas shorter photoperiods (<10 h) avoided such reductions. This suggests the potential for lower energy consumption and a reduced carbon footprint when optimizing photoperiod and spectral treatments.

The use of Light-Emitting Diode (LED) lighting as an artificial light source under controlled cultivation conditions has recently increased, aiming to improve crop yields through precise regulation of light intensity and spectral quality. A key advantage of LED systems is their ability to be adjusted to specific growth stages, thereby promoting healthier plants and maximizing productivity. Carranza-Ramírez et al. [93] demonstrated that blue light supplementation in three medicinal *C. sativa* cultivars (Calotweed, Highcol, and Souce Cauca) resulted in a significant increase in aboveground biomass—15.1% in fresh weight and 27% in dry weight—compared to exposure to white light. This effect was attributed to enhanced net photosynthesis, increased stomatal conductance, and reduced oxidative stress. In contrast, red light dominance reduced photosynthetic efficiency, possibly due to alterations in I and II photosystems, thereby limiting electron transport [118,119]. These results reinforce the essential role of blue light in maintaining photosynthetic activity and promoting healthy vegetative development in medicinal cannabis cultivars [72].

Taking these premises into account, the study’s results showed that exposure to LED2 during the vegetative stage of *C. sativa* induced alterations in the growth and development of all three cultivars. Plants developed a more compact structure with altered canopy architecture, decreased CBD levels, and elevated THC concentrations. These responses were attributed to altered photoreceptor signaling and limitations in the photosynthetic machinery, which impaired photoassimilate translocation and promoted their accumulation in aerial tissues. In contrast, LED1 treatment supported more vigorous growth, a more open canopy structure, and higher photosynthetic performance, ultimately resulting in increased CBD content. While Highcol and Souce Cauca exhibited greater vegetative growth under LED1 compared to Calotweed, no significant differences in floral production were observed among the three cultivars.

In summary, it can be stated that the selection of light spectrum plays a fundamental role in shaping the morphology, secondary metabolism, and agronomic management of *C. sativa*. Furthermore, the strategic manipulation of light spectrum—particularly the R:FR

ratio—is crucial for optimizing the development, yield, and quality of cannabis. This modulation can be effectively achieved through the use of LED lighting systems.

A balanced light spectrum featuring intensity peaks at 640 nm and 660 nm has been demonstrated to improve photosynthetic efficiency and increase floral biomass in *C. sativa*. However, excessive exposure to far-red (FR) or ultraviolet (UV) radiation can negatively impact yield, with effects varying according to genotype and the developmental stage during treatment. Manipulating the red to far-red (R:FR) ratio at specific growth phases can effectively modulate plant morphology, secondary metabolite accumulation, and energy-use efficiency, offering practical advantages for both medicinal and industrial cannabis cultivation.

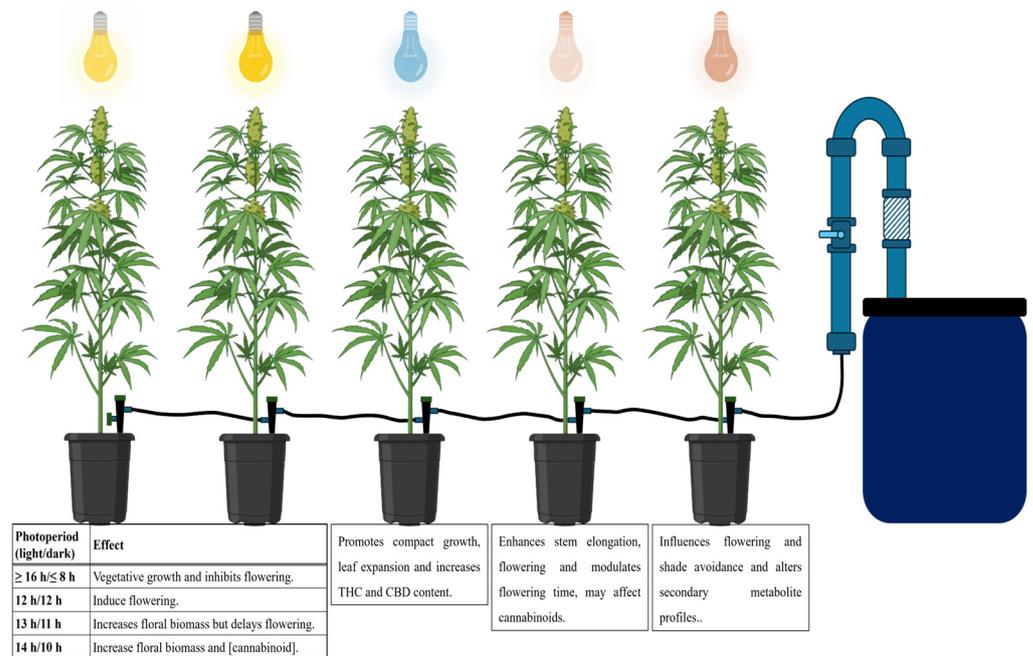
In particular, blue light supplementation appears beneficial for industrial hemp cultivars by supporting vegetative growth, while strategic application of red light pulses at key developmental milestones enhances inflorescence yield in medicinal cannabis cultivars. Although red, far-red, and blue wavelengths have been extensively characterized in *C. sativa*, recent studies point to a potential role for green light (500–570 nm) in regulating growth and signaling pathways. Furthermore, subtle differences between narrow-band LEDs—such as 640 nm versus 660 nm red light or 450 nm versus 470 nm blue light—have produced variable effects on biomass accumulation and secondary metabolite profiles. These spectral nuances remain insufficiently studied in cannabis, highlighting the need for further targeted research.

Given the notable variability in cultivars' responses and experimental conditions reported in the literature, continued systematic investigation is critical to refine and standardize light management protocols for optimized cannabis production.

Photoperiod is a crucial environmental factor influencing the flowering time, yield, and cannabinoid profile of *C. sativa* cultivars. *C. sativa* is a photoperiod-sensitive crop, aligning its development with the amount and timing of available light and, in controlled environments, requires specific lighting schedules to maintain or alter developmental phases. As a general rule, to maintain the vegetative state, growers typically use daily photoperiods of  $\geq 16$  h of light ( $\leq 8$  h of darkness), and when flowering is about to begin, the photoperiod is abruptly changed to 12 h of light and 12 h of darkness [119–121]. The standardization of photoperiod regimes for the cultivation of *C. sativa* has been established through extensive empirical research. Nevertheless, an ongoing investigation into this parameter is warranted, given the substantial genetic variability among strain/cultivar and the divergent objectives of cultivation—namely, whether the aim is industrial production or medicinal use. In order to trace the development of current understanding regarding the optimal photoperiod for this crop, the following critical review of key studies published in the last five years is reported. The review revealed that there is more research on this parameter in *C. sativa* cultivars for therapeutic use than in fiber or seed production.

Recent studies highlight that the optimal photoperiod for *C. sativa* varies significantly among cultivars, challenging the widespread assumption that a 12 h light/12 h dark regime is universally effective. Moher et al. [119] conducted a study on the flowering period of cannabis explants and found that photoperiods longer than 13.2 h prolonged the number of days to flower, with the shortest period of 12 h resulting in the fastest floral induction. Peterswald et al. [99] investigated the effects of photoperiod extension or reduction relative to the standard 12 h light/12 h dark cycle on flowering time, floral biomass production, and target cannabinoid concentrations (CBD and THC) in three medicinal cannabis cultivars: “Cannatonic”, “Northern Lights”, and “Hindu Kush”. Their goal was to identify the most efficient and productive photoperiod to maximize medicinal cannabinoid output. The results revealed genotype-specific responses to photoperiod treatments, with some cultivars showing significant yield increases under a 14 h light

regime. Most notably, the CBD-rich “Cannatonic” more than doubled its cannabinoid concentration under 14 h of light compared to the standard 12 h treatment. “Northern Lights”, one of the two THC-rich cultivars tested, exhibited a 50% increase in yield under 14 h light compared to the <12 h treatment, while “Hindu Kush” showed no significant yield change. All three cultivars showed positive morphological responses to 14 h of light at the onset of flowering, including increased height and floral biomass [99]. The variation in cultivar responses is likely due to the geographical origin of their genetic backgrounds. Thus, the assumption that a 12/12 photoperiod is universally optimal appears to be inaccurate (Figure 1). In certain cultivars, extended light periods during flowering can significantly improve yield. Optimizing the photoperiod may maximize cannabinoid concentration per inflorescence, although the optimal trade-off between yield and cannabinoid potency may differ depending on the intended medical application. Progressive photoperiod strategies—such as applying 14 h of light for the first 28 days of flowering, followed by 10 h for the remaining 29 days—have shown the potential to double yield in some cultivars [122].



**Figure 1.** Effect of photoperiod and type of light on the growth and development of *C. sativa* plants.

Studies by Ahrens et al. [49,123] show that photoperiods longer than 12 h can benefit the production of medicinal *C. sativa*, although the effects are highly dependent on the cultivar. In trials with multiple genotypes, most began flowering under up to 14 h of light, but the best floral yields were generally obtained between 12 and 13 h, with non-linear responses observed in some cultivars [49]. In cultivars such as “Incredible Milk”, a 13 h photoperiod increased floral biomass (35%) and concentrations of CBDA (+19%) and THC (+10%), whereas no significant differences were observed in others, such as “Gorilla Glue” [123]. These results highlight the potential of extended light regimes to improve productivity and cannabinoid profiles but also emphasize the need for cultivar-specific strategies due to the high variability in photoperiod sensitivity.

Although no specific wavelengths were reported, a study by Merino et al. [102] investigated the impact of photoperiod variation on the growth and cannabinoid content of *C. sativa* (var. “Cherry Oregon”) grown under field and controlled conditions in two different localities. In both locations tested, the plants with the greatest height, amount of dry biomass, biomass yield per plant, and highest biomass yield per m<sup>2</sup> were subjected

to a 3-weeklong-day (16 + 8) photoperiod treatment, compared to the plants treated for 1 or 2 weeks with the same photoperiod or those maintained under natural light. The THC and CBD contents across treatments and cycles ranged from 0.06% to 0.51% and from 13.76% to 15.29%, respectively. However, no statistically significant differences were found between the different photoperiod treatments for THC or CBD content. Slight variations were observed, with treatment 1 (16 + 8 h for 3 weeks) showing marginally higher THC and CBD in the first cycle, treatment 3 (16 + 8 h for 2 weeks) having moderately higher CBD in the second cycle, and treatment 1 again exhibiting slightly higher THC in the second cycle. These results likely reflect the importance of light radiation for photosynthesis, as insufficient light can impair plant growth and yield [102].

Photoperiod manipulation is not only critical for modifying crop traits but can also serve as a valuable tool for accelerated breeding or rapid generation cycling, aimed at fixing traits or developing hybrids [124]. This is particularly challenging, as *C. sativa* is a dioecious species [45], resulting in high levels of heterozygosity among progeny from individual crosses [125–127]. This approach, known as speed breeding, significantly shortens the plant life cycle by altering controlled environmental conditions, notably through photoperiod extension and the application of supplementary lighting, thereby enabling the completion of multiple generations per year [128]. An example of speed breeding through photoperiod modification in cannabis is reported by Schilling et al. [129], who proposed a protocol in which *C. sativa* cultivars could flower and develop seeds in less than 9 weeks. This protocol combined different photoperiods and irrigation conditions, starting with seed germination in darkness, followed by a continuous light period of approximately two weeks to promote robust vegetative growth. The protocol then proceeded to a 12 h light: 12 h dark photoperiod to induce flowering and seed development, finishing with another continuous light period and water stress to accelerate seed maturation, as outlined by Ghosh et al. [130]. The results obtained from the tested cultivars indicated high synchronization of flowering and an adequate quantity of seeds for performing crosses between cultivars and single-seed descent lines.

Photoperiod is not only relevant for biomass accumulation, cannabinoid content modulation, or speed breeding. It also determines the onset of flowering, a key factor for reproductive success [131], and is crucial for synchronizing flowering across crop cultivars, thereby facilitating the production of hybrids with intermediate traits.

The effect of photoperiod on cannabis cultivation does not extend to certain cultivars capable of flowering under continuous light conditions. These are referred to as photoperiod-independent or autoflowering cultivars, and they exhibit rapid maturation but typically present a shorter stature and reduced biomass compared to photoperiod-dependent plants [132]. Plant breeding programs have been established with the aim of crossing both photoperiod-dependent and independent cultivars to generate hybrids with intermediate traits—namely, the capacity to flower under extended photoperiods while retaining enhanced vegetative development [133–135]. Photoperiod insensitivity provides opportunities for the cultivation of *C. sativa* at higher latitudes or in controlled environments with prolonged daylight periods [132]. A representative autoflowering variety is “FINOLA”, developed in Finland for industrial purposes due to its seeds rich in essential fatty acids, which flowers independently of day length [129]. Due to the emergence of autoflowering cultivars, various investigations have been undertaken to identify the genetic basis underlying photoperiod-independent flowering. Dowling et al. [136] identified the *Autoflower2* locus, which harbors the *CsFT1* orthologue, as associated with photoperiod-insensitive flowering in hemp. Structural and expression differences in *CsFT1* among cultivars suggest that this gene plays a key role in regulating flowering independently of day length. Furthermore, the presence of at least two independent loci (*Autoflower1*

and *Autoflower2*) linked to photoperiod insensitivity indicates multiple origins of this trait in *C. sativa*, supporting the notion of a complex domestication history. In parallel, Leckie et al. [137] reported the identification of a splice site mutation in the *PSEUDO-RESPONSE REGULATOR 37* (*CsPRR37*) gene in autoflowering cannabis cultivars. This mutation disrupts the function of *CsPRR37*, a circadian clock component that typically represses expression of the *FLOWERING LOCUS T* (*FT*) gene, a key regulator of flowering. Under long-day conditions, plants carrying the mutation exhibit deregulated *CsPRR37* expression, enabling *FT* activation and thereby initiating flowering independently of the photoperiod. Altered expression of additional circadian clock genes was observed in autoflowering plants, particularly under non-inductive long-day conditions. Understanding the function of *CsPRR37* and its interaction with other circadian components is critical for manipulating flowering time and improving productivity in cannabis cultivation.

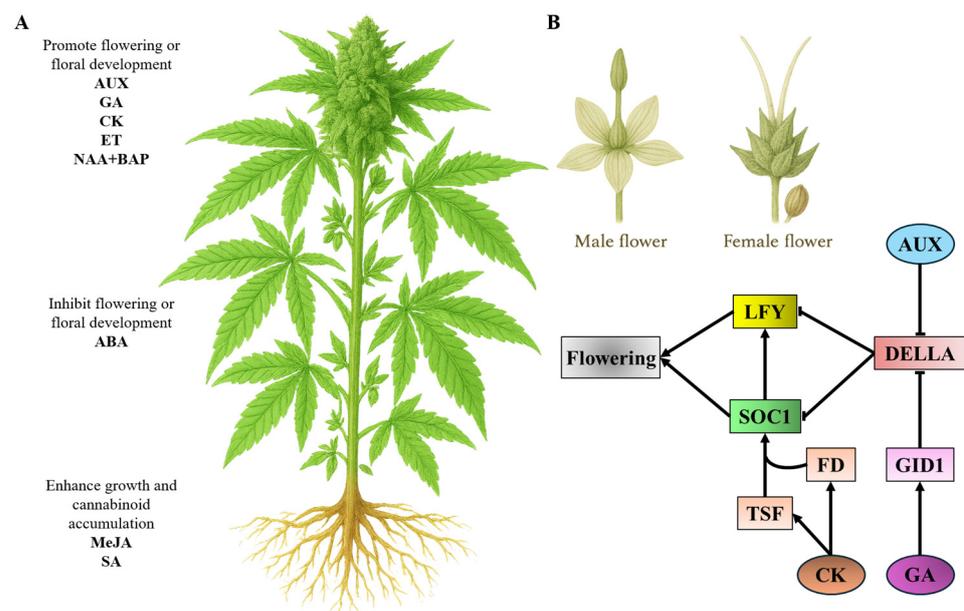
Therefore, photoperiod is a key environmental factor in the cultivation of *C. sativa*, as it regulates the onset of flowering, yield, and cannabinoid concentration. Although a 12 h light/12 h dark regime has traditionally been used to induce flowering, this approach is not optimal for all cultivars. Certain medicinal cultivars, particularly those rich in CBD, respond more favorably to extended photoperiods, exhibiting significant increases in both biomass and cannabinoid content. This response is highly genotype-dependent, underscoring the importance of tailoring photoperiod conditions to specific cultivars. Moreover, photoperiod manipulation enables the acceleration of breeding cycles through techniques such as speed breeding and facilitates the synchronization of flowering across cultivars for targeted crossing, which is especially valuable in genetic improvement programs. Additionally, there are photoperiod-insensitive cultivars, which provide opportunities for the cultivation of *C. sativa* at higher latitudes or in controlled environments with prolonged daylight periods [132]. The autoflowering trait has a complex genetic basis, associated with loci such as *Autoflower1* and *Autoflower2*, the latter of which contains an orthologue of the *FLOWERING LOCUS T* gene (*CsFT1*). Furthermore, a mutation in the *CsPRR37* gene (linked to the circadian clock) has been identified, which deregulates *FT* expression and enables daylength-independent flowering. Understanding these molecular mechanisms is crucial for manipulating flowering time and enhancing cannabis productivity in diverse growing conditions.

#### 4. Influence of Phytohormones on Floral Development and Cannabinoid Production in *C. sativa*

Floral and inflorescence development is regulated at the phytohormonal level, with hormones acting as chemical signals that coordinate processes ranging from floral induction to the formation of reproductive organs. The known functions of the different phytohormones during floral development are as follows: Abscisic Acid (ABA) suppresses both floral induction and flower formation; auxins (AUXs) promote floral induction but inhibit flower development, and under FR conditions, their synthesis is stimulated, especially in the stem [99]; gibberellins (GAs) inhibit floral induction but promote flower formation; Cytokinins (CKs) stimulate both processes; and Ethylene (ET) plays a crucial role in sex determination and floral development [138] (Figure 2).

In recent years, the exogenous application of AUXs, CKs, and GAs, as well as other phytohormones more related to defense processes, such as salicylates (SAs) and jasmonates (JAs), has been analyzed in different cultivars of *C. sativa* to determine whether these treatments result in a significant improvement in vegetative development or cannabinoid biosynthesis, i.e., their potential as plant growth regulators (PGRs). Burgel et al. [139] reported on the exogenous application of synthetic PGRs to the hemp cultivar “KANADA”, “0.2x-genetic”, and “FED”. Specifically, they analyzed naphthalene acetic acid (NAA), a

synthetic auxin, 6-benzylaminopurine (BAP), a synthetic cytokinin, and a mixture of both (NAA/BAP-mix), which were applied to apical and axillary meristems. After assessing morphology, yield, and cannabinoid content in plants with and without the different treatments, they concluded that NAA and BAP can modify plant architecture but in a genotype-specific manner. This is because NAA alone or in combination with BAP induced more compact growth in the “Kanada” genotype without compromising yield or CBD content, which could be beneficial for cultivation in limited spaces, such as *indoors*. However, these treatments were not effective for the other genotypes, and in fact, the separate or combined addition of NAA and BAP reduced inflorescence yield in these genotypes. Garrido et al. [140] tested the foliar application of stress-related phytohormones (salicylic acid (SA) and methyl jasmonate (MeJA)) and  $\gamma$ -aminobutyric acid (GABA), a non-protein amino acid involved in metabolism and stress response signaling in plants, on the medicinal cannabis cultivar “Beatriz”. This study focused on whether the application of these compounds altered the density of glandular trichomes, as these structures are where cannabinoids are predominantly synthesized and accumulated, particularly in the capitate trichomes of female flowers [47,141]. Although GABA had no effect on the “Beatriz” cultivar plants, low concentrations (0.1 mM) of SA and MeJA during the flowering phase improved growth and increased cannabinoid accumulation without affecting trichome density or the expression of key cannabinoid biosynthesis genes, suggesting that variations in cannabinoid production may not be due to these factors. These treatments could be an effective strategy for optimizing cannabinoid production in medicinal cannabis crops.



**Figure 2.** (A) Summarizing the effects of different phytohormones on the floral development of *C. sativa*. (B) Diagram showing the interaction of the phytohormones AUXs, GAs, and CKs with various transcription factors that promote flowering.

Recent studies on the effect of GA in *C. sativa* have shown that GAs regulate numerous aspects of reproductive development, and their effect can be promotive, nonexistent, or inhibitory. GAs are essential for plant growth and development, including stem elongation, seed germination, and flowering [142], and promote flowering under short-day conditions by activating genes such as *SOC1* (Suppressor of Overexpression of *CONSTANS1*) and *LFY* (*leafy*), which are essential for floral transition, especially when the photoperiod pathway is not active [143]. AUX, GA, and CK promote flowering through their interaction with the transcription factors *SOC1* and *LFY*, which are involved in floral induction

in the shoot apical meristem (SAM) and in floral development and identity acquisition, respectively [144–146]. AUX and GA, upon binding to their receptor GID1 (Gibberellin Insensitive Dwarf1), act by inhibiting DELLA, a negative regulator of transcription factors, including SOC1 and LFY. On the other hand, CKs activate FD (a bZIP transcription factor) and TSF (Twin Sister of FT), which in turn enhance SOC1 activity [147].

In cannabis, Alter et al. [148] conducted a study where they combined hormonal treatment (with AUX and GA) with different photoperiods (long day (16 + 8) vs short day (12 + 12)) in a medicinal cannabis cultivar. Their results indicated that exposure to at least three consecutive days of short photoperiod was required to initiate inflorescence development, which they associated with a decrease in GA and AUX levels at the shoot apex, coinciding with the formation of compact inflorescences. When the photoperiod was switched to long day, there was an increase in GA and AUX levels, leading to disorganization of the inflorescences and resumption of vegetative growth. Exogenous GA application under short-day conditions prevented inflorescence development, while AUX application had no significant effect under any condition. This is consistent with observations in *Solanum lycopersicum*, *Fuchsia*, and *Pisum sativum*, where exogenous GA application delayed flowering time [149–151]. Therefore, it can be deduced that GAs play a crucial role in mediating photoperiodic signals that regulate inflorescence development in female cannabis plants. It was also concluded that a decrease in GA and AUX under short-day conditions is essential for the formation of compact inflorescences, while elevated levels of these hormones favor vegetative growth. These findings provide a foundation for cultivation strategies that optimize plant architecture and flower production in cannabis. Furthermore, in cannabis, GA also plays a role in sex determination, although it is infrequently used for feminized seed production, as improper concentrations can promote the initiation of male flowers in female plants [152,153].

Thus, the use of exogenous phytohormones, such as GA, AUX, and other stress-related compounds, has a significant impact on the vegetative and reproductive development of *C. sativa*. However, it is crucial to adjust hormonal treatments according to genotype and environmental conditions to achieve optimal results, especially in the enhancement of cannabinoid production and controlled flowering.

## 5. Integrated Cultivation Methods for *C. sativa* Balancing Production Quality

*C. sativa* can be cultivated using a range of production systems, including phytotron facilities, indoor setups, open-field cultivation, greenhouses, and in vitro tissue culture. The choice of cultivation method primarily depends on two factors: the intended purpose and the applicable regulatory framework. For industrial hemp, open-field cultivation is generally preferred due to its lower cost and suitability for large-scale production of fiber and/or seeds. However, this method is subject to environmental challenges such as adverse weather conditions, pathogens, and the risk of genetic contamination through unintended cross-pollination. Therefore, to facilitate cultivation under uniform environmental conditions and ensure a homogeneous product—by reducing the influence of environmental factors that shape plant physiological processes, thereby affecting phenotypic expression, the production of primary and secondary metabolites, and even interspecific variability—there is a growing trend towards cultivating cannabis in controlled environments, such as greenhouses, indoor facilities, or through in vitro methods [154]. The cultivation of medicinal cannabis in indoor environments and greenhouses offers advantages such as climate control, security, and precise regulation of environmental factors such as light, temperature, humidity, CO<sub>2</sub>, and nutrients, allowing for the establishment of optimal conditions for continuous, high-yield production with greater consistency and reliability

in product quality [155,156]. However, this type of cultivation can also induce thermal or light stress, particularly in the absence of supplemental lighting to complement natural radiation or when the greenhouse covering filters UV-B radiation, which can reduce the synthesis of antioxidant compounds such as polyphenols [154,157,158]. In recent years, the adoption of LED technology has increased due to its adaptability to the specific needs of the crop [155].

On the other hand, this system can be complemented with hydroponic cultivation. Hydroponics offers significant advantages over soil-based cultivation. Yield per unit area and the number of crop cycles per year can be increased due to the precise control over nutrient delivery—both in terms of composition and timing according to the plant's developmental stage—as well as regulation of pH and environmental conditions [159]. This system enables a much more efficient use of water and fertilizers, significantly reduces the incidence of soil-borne pests and diseases, and optimizes growing space through vertical structures. The potential for automation would reduce the need for manual labor and improve the consistency of results while also minimizing the environmental impact associated with soil degradation and the excessive use of agrochemicals. This system could be highly effective for industrial or medicinal cannabis cultivation, as it would help standardize growing conditions—something particularly relevant for a species with high genetic and phenotypic variability, such as cannabis. Such standardization may enhance both the economic feasibility of cultivation and support plant breeding programs. However, thorough research is required to determine the most suitable conditions for each crop, and within each crop, the effects on different cultivars must be carefully evaluated.

Bafort et al. [159] showed that hydroponic cultivation in greenhouses, combined with the application of the growth regulator Ethephon, can significantly improve the agronomic performance of industrial *C. sativa* cultivars compared to open-field cultivation. While the treatment increased biomass and structural development in both varieties, its impact on cannabinoid synthesis was variable: Whereas Cannabigerol (CBG) levels in “Santhica 27” remained consistent, the total CBD concentration in “Felina 32” was lower in the greenhouse. Despite this, the hydroponic system demonstrated potential for increasing the annual cannabinoid yield. However, the high costs associated with this method highlight the need for optimization, particularly through the integration of supplemental lighting, automation of systems, and adjustments to biomodulator doses. These results suggest that intensive greenhouse approaches can be effective but require cultivar-specific strategies and a rigorous cost-benefit analysis. A low-cost alternative that ensures basic controlled conditions is the “high tunnel”. This is a simple type of greenhouse without thermal regulation or heating systems, but it creates a favorable microclimate for plant growth, health, and quality. High tunnels offer protection against extreme weather conditions, pathogens, and pests by establishing a controlled environment, and they also extend the harvest season at a significantly lower cost compared to high-tech greenhouses [160,161]. This system is becoming more and more widespread in the United States for growing fruits and vegetables such as tomatoes, watermelons, strawberries, and cucumbers [162–165], generating an increase in biomass, better fruit quality, and greater profitability compared to open field production [162]. In relation to industrial cannabis, the implementation of such practices could lead to improved management of pests, diseases, and water resources, thereby contributing to high floral yields—crucial for the production of cannabinoids and terpenes. In a study involving industrial cannabis cultivars (SB1 and CJ2) with high CBD content, the use of such facilities significantly improved total biomass, stem number, and diameter, and resulted in high CBD levels in early harvests. However, THC levels remained below the legal threshold [161].

*Indoor* and *in vitro* cultivation are good alternatives to develop parental lines or fix characters to be able to develop hybrids in greenhouses or open fields, where variability is greater and can affect or hinder the identification and isolation of pure lines.

*Indoor* cannabis cultivation involves higher infrastructure and energy costs compared to *outdoor* or greenhouse production but allows growers to fully control the growing environment, including photoperiod. This facilitates consistent production cycles with respect to duration, yield, and product quality. The main objective of *indoor* cannabis production is to obtain cannabinoid-rich floral tissues, and it is crucial to elicit strong and consistent flowering responses. *Indoor* cannabis cultivation usually starts with a vegetative growth period under long photoperiods (over 16 h). Once the plants reach a suitable size, they are transferred to the flowering phase, using a short daytime photoperiod, typically 12 h [166]. The use of a 12 h photoperiod has been widely adopted in the *indoor* cannabis cultivation industry because of its ability to induce rapid and robust flowering responses in photoperiod-sensitive cannabis cultivars [129]. However, it is also recognized that environmental conditions and plant management strategies, such as growth substrate, water restriction, light spectrum, and plant architecture formation, can influence cannabinoid accumulation [167,168]. Maintaining controlled conditions in medical cannabis production is essential to ensure consistent production, both in terms of inflorescence yield and concentrations of the plant's specialized metabolites. Since unprocessed inflorescences are administered directly to patients, it is crucial to achieve uniform concentrations of these metabolites [169,170]. In these environments, radiation is provided by artificial lighting. Since cannabis is a short-day plant, artificial light must meet specific energy requirements for photosynthesis [63]. The growing global expansion of the medicinal cannabis industry highlights the need for more energy-efficient lighting systems [111]. Currently, several types of lighting are used in agriculture and the cannabis industry, including high-intensity discharge (HID) lamps, such as metal halide (MH) and high-pressure sodium (HPS) lamps, fluorescent lights, and LEDs. These lighting types vary in intensity and spectrum [63]. LED technology offers advantages such as higher energy efficiency, longer lifespan, and the ability to adjust the light spectrum while maintaining high levels of PPFD with lower heat emission. This allows for more effective light control to optimize plant production and biomass development [171–174]. In particular, with LED lights, the red–blue ratio can be modified, something important in horticultural applications, since it significantly affects dry matter production and plant development [90,91]. One of the potential drawbacks of *indoor* cultivation is the high energy demand associated with this method, as well as the resulting greenhouse gas emissions [175]. Therefore, adopting open-field or energy-efficient greenhouse cultivation practices may offer a viable solution to substantially reduce the industry's carbon footprint [175].

Among the types of cultivation systems analyzed, it is also important to emphasize that planting density significantly influences cannabinoid biosynthesis and the pruning regime applied. For instance, when planting density exceeds 1–2 plants/m<sup>2</sup>, the cannabinoid concentration per plant tends to decrease, while the yield per unit area increases [176,177]. The removal of primary and secondary branches enhances the uniformity of cannabinoid concentration throughout the plant by increasing levels in its lower parts [63].

Within *in vitro* cultivation, tissue culture has gained prominence as a valuable tool for the maintenance and genetic propagation of cannabis, offering advantages such as sterile growing conditions, mass propagation potential, and preservation of genetic traits [178,179]. Micropropagation is typically conducted under long photoperiods (16–18 h of light per day) to maintain plants in a vegetative state [119]. However, certain cannabis genotypes have been observed to initiate flowering *in vitro* even under extended photoperiods, presenting new opportunities to investigate the regulation of secondary metabolism and floral organo-

genesis for regeneration purposes, as well as to rapidly identify genotype-specific critical photoperiods [119,180]. While in vitro flowering is well documented in other short-day species such as tobacco, it remains sporadic and poorly understood in cannabis. Furthermore, it is unclear whether in vitro photoperiodic responses correspond with those observed in whole plants. The flowering of some cannabis genotypes under long-day in vitro conditions suggests that additional factors—such as plant growth regulators [181], day/night temperature regimes, and other environmental variables [182]—may influence flowering responses. Future research should focus on validating these results in whole plants to refine the understanding of critical photoperiod thresholds. Additionally, the application of tissue culture could help growers optimize production cycles, save space and time, and support the development of in vitro models for investigating flowering regulation and metabolite expression.

Consequently, there are various cultivation alternatives available for different cannabis cultivars. The selection of a particular system—open-field, greenhouse, indoor, in vitro culture, or high tunnels—depends both on the intended purpose of production (industrial or medicinal) and the prevailing regulatory framework. Open-field cultivation is more cost-effective and generally suited to industrial hemp, though it is subject to environmental factors that may affect product uniformity [183,184]. Conversely, cultivation in controlled environments such as greenhouses or indoor facilities allows for the optimization of environmental variables (light, temperature, humidity, and nutrients), thereby improving product quality and consistency, albeit with higher energy and infrastructure costs.

Greenhouse-based hydroponic cultivation has been shown to enhance several agronomic parameters and may be especially advantageous for achieving production standardization in genetically variable cultivars. Additionally, technologies such as LED lighting—enabling the spectral tuning of light to influence cannabinoid profiles—and the use of growth regulators such as Ethephon are being explored. In vitro micropropagation is also considered a useful tool for genetic conservation and the production of parental lines, although its direct commercial application remains limited.

Overall, the optimal approach appears to be a combination of environmental control, energy efficiency, and compliance with the legal framework, taking into account both economic and environmental sustainability.

## 6. Final Considerations and Future Perspectives

*C. sativa* is a species with significant medicinal potential due to its production of compounds derived from secondary metabolism, namely the cannabinoids. The primary types of cannabinoids are THC, CBD, and CBG, with the former being the limiting factor for its cultivation and use due to its psychoactive properties, as determined by the legislation of the country in which it is grown. All of these cannabinoids possess therapeutic properties. However, there are cannabis cultivars with low cannabinoid production intended for use in industries such as food and textiles.

Moreover, it is a highly valuable species in the agricultural sector due to its potential use in crop rotation systems, its capacity to improve soil conditions, and its ability to remove xenobiotic compounds from the soil, such as heavy metals (bioremediation).

Given its versatility in terms of potential applications, it is essential to further investigate the optimal cultivation practices for the different existing cultivars. Numerous studies have been conducted, particularly in the last decade, examining facilities, types of radiation, and photoperiod regimes in order to standardize its cultivation. Nonetheless, due to the wide array of genotypes and their influence on plant development and cannabinoid biosynthesis, continued research on this species is necessary. Generally, it is known that a 12:12 light–dark photoperiod is the most commonly used regime, though it is not suitable

for all cultivars, especially for autoflowering types whose development is independent of day length.

Similarly, the light spectrum, particularly the red to R:FR ratio, plays a critical role in optimizing both development and cannabinoid production. Increased blue light application may be especially advantageous for industrial cultivars, whereas in medicinal cannabis, the use of red light pulses at specific developmental stages may prove more effective. The same applies to the cultivation system. Open-field cultivation is more cost-effective and suitable for industrial hemp, although it is exposed to environmental factors that can compromise product uniformity. In contrast, cultivation in controlled environments such as greenhouses or indoor facilities allows for optimization of environmental variables (light, temperature, humidity, and nutrients), thus improving both quality and consistency of the final product. This is particularly true when combined with hydroponic systems and LED lighting, which are most appropriate for medicinal cannabis.

The exogenous application of phytohormones such as gibberellins (GAs) or auxins (AUXs) may positively influence flowering and cannabinoid synthesis; however, as with other parameters, these effects vary between different cultivars.

Thus, due to the considerable variability reported across studies on this species, techniques such as micropropagation are essential for evaluating genotypic differences and understanding why cultivars intended for the same purpose may respond differently under similar conditions.

Despite recent advances, several gaps remain in our understanding of photoperiod and spectral regulation in *C. sativa*. Key challenges include the high genetic variability among cultivars, inconsistent results across photobiological studies, and limited data on emerging light spectra such as green and narrow-band LEDs. Future research should aim to elucidate genotype-specific light responses, explore hormonal cross-talk under artificial lighting, and integrate omics-based approaches to link light cues to cannabinoid biosynthesis pathways. Developing standardized cultivation protocols will also be crucial for advancing commercial applications.

One particular area that requires further investigation is the effect of blue light on CBD biosynthesis, which has yielded inconsistent results across studies. These discrepancies may stem from genotypic differences between THC- and CBD-dominant cultivars, variation in environmental parameters such as light intensity and photoperiod duration, and indirect effects mediated by trichome development or oxidative stress responses. A more systematic comparison of experimental designs is needed to elucidate the mechanisms involved and resolve the contradictory findings.

**Author Contributions:** A.S.: Writing—original draft. A.C.S.: Writing—bibliographic search; review; and editing. C.M.R.V.: Supervision; writing—review and editing. P.M.: Supervision; writing—review and editing. A.O.: Writing—bibliographic search; Supervision; review and editing. A.I.C.: Supervision; review and editing. J.T.d.G.: Supervision; review and editing. All authors have read and agreed to the published version of the manuscript.

**Funding:** This work was supported by national funds through the Foundation for Science and Technology, I.P. (Portuguese Foundation for Science and Technology) by the project UIDB/05064/2023 (VALORIZA-Research Center for Endogenous Resource Valorization). Project 0066\_BGREENER\_4\_E is co-financed by the European Union through the Interreg VI-A Spain–Portugal Program (POCTEP) 2021–2027. Patrick Materatski's contract was supported by Portuguese National Funds through FCT/MCTES, under the CEEC (<https://doi.org/10.54499/2021.01553.CEECIND/CP1670/CT0003>). The authors also thank the support of CERNAS-UIDB/00681 (<https://doi.org/10.54499/UIDP/00681/2020>), MED-UIDB/05183 (<https://doi.org/10.54499/UIDB/05183/2020>; <https://doi.org/10.54499/UIDP/05183/2020>) and CHANGE (<https://doi.org/10.54499/LA/P/0121/2020>).

**Data Availability Statement:** Data sharing not applicable to this article, as no data sets were generated or analyzed during the current study.

**Conflicts of Interest:** Author Ana Cláudia Silva was employed by the company Compañía Extremeña de Investigación y Producción Agroalimentaria S.A. The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## Abbreviations

The following abbreviations are used in this manuscript:

<i>C. sativa</i>	<i>Cannabis sativa</i>
THC	$\Delta^9$ -tetrahydrocannabinol
CBD	Cannabidiol
ECS	Endocannabinoid System
CRC	Colorectal Cancer
CBDA	Cannabidiolic Acid
THCA	Tetrahydrocannabinolic Acid
CBGA	Cannabigerolic Acid
CBG	Cannabigerol
CBCA	Cannabichromenic Acid
CO <sub>2</sub>	Carbon Dioxide
PAR	Photosynthetically Active Radiation
UVA	Ultraviolet-A
ROS	Reactive Oxygen Species
LUE	Light Use Efficiency
FR	Far-Red
R:FR	Red to Far-Red
PPFD	Photosynthetic Photon Flux Density
UV	Ultraviolet
LED	Light-Emitting Diode
CsPRR37	<i>Cannabis sativa</i> Pseudo-Response Regulator 37
FT	FLOWERING LOCUS T
CsFT1	<i>Cannabis sativa</i> FLOWERING LOCUS T gene
ABA	Abscisic Acid
AUXs	Auxins
GAs	Gibberellins
CKs	Cytokinins
ET	Ethylene
SAs	Salicylates
JAs	Jasmonates
PGRs	Plant Growth Regulators
NAA	Naphthalene Acetic Acid
BAP	6-Benzylaminopurine
SaA	Salicylic Acid
MeJA	Methyl Jasmonate
GABA	$\gamma$ -Aminobutyric Acid
SOC1	Suppressor of Overexpression of Constans1
UV-B	Ultraviolet-B
HID	High-Intensity Discharge
MH	Metal Halide
HPS	High-Pressure Sodium

## References

1. El Oihabi, M.; Sultana, M.; Ammari, M.; Ben Allal, L.; Fakhri Lanjri, A. Diversity and variability of bioactive compounds in *Cannabis sativa*: Effects on therapeutic and environmental uses and orientations for future research. *Case Stud. Chem. Environ. Eng.* **2024**, *9*, 100732. [[CrossRef](#)]
2. Pollio, A. The Name of *Cannabis*: A Short Guide for Nonbotanists. *Cannabis Cannabinoid Res.* **2016**, *1*, 234–238. [[CrossRef](#)] [[PubMed](#)]
3. Lamarck, J.B. *Encyclopédie Méthodique. Botanique*; Panckoucke: Paris, France, 1783.
4. Janischevsky, D.E. A form of hemp in wild areas of southeastern Russia. *NG Cern. Univ.* **1924**, *2*, 3–17.
5. Small, E.; Cronquist, A. A Practical and Natural Taxonomy for Cannabis. *Taxon* **1976**, *25*, 405–435. [[CrossRef](#)]
6. Small, E. Evolution and Classification of *Cannabis sativa* (Marijuana, Hemp) in Relation to Human Utilization. *Bot. Rev.* **2015**, *81*, 189–294. [[CrossRef](#)]
7. Trancoso, I.; De Souza, G.A.R.; Dos Santos, P.R.; Dos Santos, K.D.; De Miranda, R.M.D.S.N.; Da Silva, A.L.P.M.; Santos, D.Z.; García-Tejero, I.F.; Campostrini, E. *Cannabis sativa* L. Crop Management and Abiotic Factors That Affect Phytocannabinoid Production. *Agronomy* **2022**, *12*, 1492. [[CrossRef](#)]
8. Wani, K.A.; Andrabhi, S.J.; Manzoor, J.; Qadir, H.; Jan, K. Cultivation of Cannabis: Medicinal, Social, and Legal Aspects. In *Cannabis sativa Cultivation, Production, and Applications in Pharmaceuticals and Cosmetics*; IGI Global Scientific Publishing: Hershey, PA, USA, 2023; pp. 43–51.
9. Rupasinghe, H.P.V.; Davis, A.; Kumar, S.K.; Murray, B.; Zheljzkov, V.D. Industrial Hemp (*Cannabis sativa* subsp. *sativa*) as an Emerging Source for Value-Added Functional Food Ingredients and Nutraceuticals. *Molecules* **2020**, *25*, 4078. [[CrossRef](#)] [[PubMed](#)]
10. Saloner, A.; Bernstein, N. Nitrogen Source Matters: High NH<sub>4</sub>/NO<sub>3</sub> Ratio Reduces Cannabinoids, Terpenoids, and Yield in Medical Cannabis. *Front. Plant Sci.* **2022**, *13*, 830224. [[CrossRef](#)]
11. Cockson, P.; Schroeder-Moreno, M.; Veazie, P.; Barajas, G.; Logan, D.; Davis, M.; Whipker, B.E. Impact of Phosphorus on *Cannabis sativa* Reproduction, Cannabinoids, and Terpenes. *Appl. Sci.* **2020**, *10*, 7875. [[CrossRef](#)]
12. Shiponi, S.; Bernstein, N. Response of medical cannabis (*Cannabis sativa* L.) genotypes to P supply under long photoperiod: Functional phenotyping and the ionome. *Ind. Crops Prod.* **2021**, *161*, 113154. [[CrossRef](#)]
13. Radwan, M.M.; Chandra, S.; Gul, S.; ElSohly, M.A. Cannabinoids, Phenolics, Terpenes and Alkaloids of Cannabis. *Molecules* **2021**, *26*, 2774. [[CrossRef](#)]
14. Oriola, A.O.; Kar, P.; Oyediji, A.O. *Cannabis sativa* as an Herbal Ingredient: Problems and Prospects. *Molecules* **2024**, *29*, 3605. [[CrossRef](#)] [[PubMed](#)]
15. Fordjour, E.; Manful, C.F.; Sey, A.A.; Javed, R.; Pham, T.H.; Thomas, R.; Cheema, M. Cannabis: A multifaceted plant with endless potentials. *Front. Pharmacol.* **2023**, *14*, 1200269. [[CrossRef](#)]
16. Lowe, H.; Toyang, N.; Steele, B.; Bryant, J.; Ngwa, W. The Endocannabinoid System: A Potential Target for the Treatment of Various Diseases. *Int. J. Mol. Sci.* **2021**, *22*, 9472. [[CrossRef](#)]
17. Grosso, A.F. Cannabis: From plant condemned by prejudice to one of the greatest therapeutic options of the century. *J. Hum. Growth Dev.* **2020**, *30*, 94–97. [[CrossRef](#)]
18. Pratt, M.; Stevens, A.; Thuku, M.; Butler, C.; Skidmore, B.; Wieland, L.S.; Clemons, M.; Kanji, S.; Hutton, B. Benefits and harms of medical cannabis: A scoping review of systematic reviews. *Syst. Rev.* **2019**, *8*, 320. [[CrossRef](#)]
19. Citti, C.; Braghiroli, D.; Vandelli, M.A.; Cannazza, G. Pharmaceutical and biomedical analysis of cannabinoids: A critical review. *J. Pharm. Biomed. Anal.* **2018**, *147*, 565–579. [[CrossRef](#)] [[PubMed](#)]
20. Russo, E.B. Taming THC: Potential cannabis synergy and phytocannabinoid-terpenoid entourage effects. *Br. J. Pharmacol.* **2011**, *163*, 1344–1364. [[CrossRef](#)] [[PubMed](#)]
21. Vučković, S.; Srebro, D.; Vujović, K.; Vučetić, C.; Prostran, M. Cannabinoids and Pain: New Insights from Old Molecules. *Front. Pharmacol.* **2018**, *9*, 1259. [[CrossRef](#)]
22. Liktör-Busa, E.; Keresztes, A.; LaVigne, J.; Streicher, J.; Largent-Milnes, T. Analgesic Potential of Terpenes Derived from *Cannabis sativa*. *Pharmacol. Rev.* **2021**, *73*, 98–126. [[CrossRef](#)]
23. McDougall, J.J.; McKenna, M.K. Anti-Inflammatory and Analgesic Properties of the Cannabis Terpene Myrcene in Rat Adjuvant Monoarthritis. *Int. J. Mol. Sci.* **2022**, *23*, 7891. [[CrossRef](#)]
24. Atalay, S.; Jarocka-Karpowicz, I.; Skrzydlewska, E. Antioxidative and Anti-Inflammatory Properties of Cannabidiol. *Antioxidants* **2019**, *9*, 21. [[CrossRef](#)] [[PubMed](#)]
25. Silva-Reis, R.; Silva, A.M.S.; Oliveira, P.A.; Cardoso, S.M. Antitumor Effects of *Cannabis sativa* Bioactive Compounds on Colorectal Carcinogenesis. *Biomolecules* **2023**, *13*, 764. [[CrossRef](#)]
26. De Medeiros Dantas, J.M.; Chastel, C.F.; Wolfaardt, F.J.; Ghislain, T.; Lavoie, J.-M. Cannabis-based biofuels in a biorefinery approach. *Ind. Crops Prod.* **2023**, *204*, 117225. [[CrossRef](#)]
27. Tahir, M.N.; Shahbazi, F.; Rondeau-Gagné, S.; Trant, J.F. The biosynthesis of the cannabinoids. *J. Cannabis Res.* **2021**, *3*, 7. [[CrossRef](#)]

28. Krejčí, Z.; Šantavý, F. The isolation of further substances from the leaves of Indian hemp (*Cannabis sativa* L., var. *indica*). *Acta Univ. Palacki. Olomuc. Fac. Med.* **1955**, *6*, 59–66.
29. DeCarcer, G.A.; Kagia, J.; Morrissey, K.; McCann, M.; Tomares, N.; Alvarado, I.; McCoy, J.J.; Watkins, E. *The Global Cannabis Report*; New Frontier Data: Washington, DC, USA, 2021.
30. Prohibition Partners. *The Global Cannabis Report: 5th Edition (Updated)*; PP Intelligence Ltd.: London, UK, 2024.
31. Russo, E.B. The Case for the Entourage Effect and Conventional Breeding of Clinical Cannabis: No “Strain,” No Gain. *Front. Plant Sci.* **2019**, *9*, 1969. [[CrossRef](#)]
32. Naeem, M.Y.; Corbo, F.; Crupi, P.; Clodoveo, M.L. Hemp: An Alternative Source for Various Industries and an Emerging Tool for Functional Food and Pharmaceutical Sectors. *Processes* **2023**, *11*, 718. [[CrossRef](#)]
33. Bertoli, A.; Tozzi, S.; Pistelli, L.; Angelini, L.G. Fibre hemp inflorescences: From crop-residues to essential oil production. *Ind. Crops Prod.* **2010**, *32*, 329–337. [[CrossRef](#)]
34. Strzelczyk, M.; Lochynska, M.; Chudy, M. Systematics and Botanical Characteristics of Industrial Hemp *Cannabis sativa* L. *J. Nat. Fibers* **2022**, *19*, 5804–5826. [[CrossRef](#)]
35. Sorrentino, G. Introduction to emerging industrial applications of cannabis (*Cannabis sativa* L.). *Rend. Lincei Sci. Fis. E Nat.* **2021**, *32*, 233–243. [[CrossRef](#)]
36. Yano, H.; Fu, W. Hemp: A Sustainable Plant with High Industrial Value in Food Processing. *Foods* **2023**, *12*, 651. [[CrossRef](#)]
37. Kaur, G.; Kander, R. The Sustainability of Industrial Hemp: A Literature Review of Its Economic, Environmental, and Social Sustainability. *Sustainability* **2023**, *15*, 6457. [[CrossRef](#)]
38. Tang, L.; Fan, C.; Yuan, H.; Wu, G.; Sun, J.; Zhang, S. The Effect of Rotational Cropping of Industrial Hemp (*Cannabis sativa* L.) on Rhizosphere Soil Microbial Communities. *Agronomy* **2022**, *12*, 2293. [[CrossRef](#)]
39. Visković, J.; Zheljzkov, V.D.; Sikora, V.; Noller, J.; Latković, D.; Ocamb, C.M.; Koren, A. Industrial Hemp (*Cannabis sativa* L.) Agronomy and Utilization: A Review. *Agronomy* **2023**, *13*, 931. [[CrossRef](#)]
40. Kok, C.J.; Coenen, G.C.M.; de Heij, A. The effect of fibre hemp (*Cannabis sativa* L.) on selected soil-borne pathogens. *J. Int. Hemp Assoc.* **1994**, *1*, 6–9.
41. Flajšman, M.; Košmelj, K.; Grčman, H.; Ačko, D.K.; Zupan, M. Industrial hemp (*Cannabis sativa* L.)—A valuable alternative crop for growing in agricultural soils contaminated with heavy metals. *Environ. Sci. Pollut. Res.* **2023**, *30*, 115414–115429. [[CrossRef](#)] [[PubMed](#)]
42. Charkowski, E. Hemp ‘Eats’ Chernobyl Waste. Available online: <https://rediscoverhemp.thisfemmedaddy.com/inspire/hemp-eats-chernobyl-waste-offers-hope-for-hanford/> (accessed on 18 February 2022).
43. Golia, E.E.; Bethanis, J.; Ntinopoulos, N.; Kaffe, G.-G.; Komnou, A.A.; Vasilou, C. Investigating the potential of heavy metal accumulation from hemp. The use of industrial hemp (*Cannabis sativa* L.) for phytoremediation of heavily and moderated polluted soils. *Sustain. Chem. Pharm.* **2023**, *31*, 100961. [[CrossRef](#)]
44. Kraszkiewicz, A.; Kachel, M.; Parafiniuk, S.; Zając, G.; Niedziółka, I.; Sprawka, M. Assessment of the Possibility of Using Hemp Biomass (*Cannabis sativa* L.) for Energy Purposes: A Case Study. *Appl. Sci.* **2019**, *9*, 4437. [[CrossRef](#)]
45. Schilling, J.M.; Hughes, C.G.; Wallace, M.S.; Sexton, M.; Backonja, M.; Moeller-Bertram, T. Cannabidiol as a Treatment for Chronic Pain: A Survey of Patients’ Perspectives and Attitudes. *J. Pain Res.* **2021**, *14*, 1241–1250. [[CrossRef](#)]
46. Johnson, N. American Weed: A History of Cannabis Cultivation in the United States. *EchoGéo* **2019**, *48*, 1–22. [[CrossRef](#)]
47. Tanney, C.A.S.; Backer, R.; Geitmann, A.; Smith, D.L. Cannabis Glandular Trichomes: A Cellular Metabolite Factory. *Front. Plant Sci.* **2021**, *12*, 721986. [[CrossRef](#)]
48. Cermeño, Z.S. *Construcción de Invernaderos*; MundiPrensa: Madrid, Spain, 2005.
49. Ahrens, A.; Llewellyn, D.; Zheng, Y. Is Twelve Hours Really the Optimum Photoperiod for Promoting Flowering in Indoor-Grown Cultivars of *Cannabis sativa*? *Plants* **2023**, *12*, 2605. [[CrossRef](#)]
50. Chandra, S.; Lata, H.; Khan, I.A.; Elsohly, M.A. Photosynthetic response of *Cannabis sativa* L. to variations in photosynthetic photon flux densities, temperature and CO<sub>2</sub> conditions. *Physiol. Mol. Biol. Plants* **2008**, *14*, 299–306. [[CrossRef](#)]
51. Magagnini, G.; Grassi, G.; Kotiranta, S. The Effect of Light Spectrum on the Morphology and Cannabinoid Content of *Cannabis sativa* L. *Med. Cannabis Cannabinoids* **2018**, *1*, 19–27. [[CrossRef](#)] [[PubMed](#)]
52. Reichel, P.; Munz, S.; Hartung, J.; Präger, A.; Kotiranta, S.; Burgel, L.; Schober, T.; Graeff-Hönninger, S. Impact of Three Different Light Spectra on the Yield, Morphology and Growth Trajectory of Three Different *Cannabis sativa* L. Strains. *Plants* **2021**, *10*, 1866. [[CrossRef](#)]
53. Rodriguez-Morrison, V.; Llewellyn, D.; Zheng, Y. Cannabis Yield, Potency, and Leaf Photosynthesis Respond Differently to Increasing Light Levels in an Indoor Environment. *Front. Plant Sci.* **2021**, *12*, 646020. [[CrossRef](#)]
54. Park, S.-H.; Pauli, C.S.; Gostin, E.L.; Staples, S.K.; Seifried, D.; Kinney, C.; Vanden Heuvel, B.D. Effects of short-term environmental stresses on the onset of cannabinoid production in young immature flowers of industrial hemp (*Cannabis sativa* L.). *J. Cannabis Res.* **2022**, *4*, 1. [[CrossRef](#)]

55. Morgan, W.; Singh, J.; Kesheimer, K.; Davis, J.; Sanz-Saez, A. Severe drought significantly reduces floral hemp (*Cannabis sativa* L.) yield and cannabinoid content but moderate drought does not. *Environ. Exp. Bot.* **2024**, *219*, 105649. [CrossRef]
56. Dilena, E.; Close, D.C.; Hunt, I.; Garland, S.M. Investigating how nitrogen nutrition and pruning impacts on CBD and THC concentration and plant biomass of *Cannabis sativa*. *Sci. Rep.* **2023**, *13*, 19533. [CrossRef] [PubMed]
57. Pennisi, G.; Pistillo, A.; Orsini, F.; Cellini, A.; Spinelli, F.; Nicola, S.; Fernandez, J.A.; Crepaldi, A.; Gianquinto, G.; Marcelis, L.F.M. Optimal light intensity for sustainable water and energy use in indoor cultivation of lettuce and basil under red and blue LEDs. *Sci. Hortic.* **2020**, *272*, 109508. [CrossRef]
58. Ouzounis, T.; Rosenqvist, E.; Ottosen, C.-O. Spectral Effects of Artificial Light on Plant Physiology and Secondary Metabolism: A Review. *HortScience* **2015**, *50*, 1128–1135. [CrossRef]
59. Azcón-Bieto, J.; Talón, M. *Fundamentos de Fisiología Vegetal*; McGraw-Hill—Interamericana de España, S.L.: Madrid, Spain, 2000.
60. Shi, Y.; Ke, X.; Yang, X.; Liu, Y.; Hou, X. Plants response to light stress. *J. Genet. Genom.* **2022**, *49*, 735–747. [CrossRef]
61. Evans, J.R.; Poorter, H. Photosynthetic acclimation of plants to growth irradiance: The relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. *Plant Cell Environ.* **2001**, *24*, 755–767. [CrossRef]
62. Bian, Z.H.; Yang, Q.C.; Liu, W.K. Effects of light quality on the accumulation of phytochemicals in vegetables produced in controlled environments: A review: Effects of light on vegetable phytochemicals. *J. Sci. Food Agric.* **2015**, *95*, 869–877. [CrossRef]
63. Danziger, N.; Bernstein, N. Light matters: Effect of light spectra on cannabinoid profile and plant development of medical cannabis (*Cannabis sativa* L.). *Ind. Crops Prod.* **2021**, *164*, 113351. [CrossRef]
64. Tan, T.; Li, S.; Fan, Y.; Wang, Z.; Ali Raza, M.; Shafiq, I.; Wang, B.; Wu, X.; Yong, T.; Wang, X.; et al. Far-red light: A regulator of plant morphology and photosynthetic capacity. *Crop J.* **2022**, *10*, 300–309. [CrossRef]
65. Paik, I.; Huq, E. Plant photoreceptors: Multi-functional sensory proteins and their signaling networks. *Semin. Cell Dev. Biol.* **2019**, *92*, 114–121. [CrossRef] [PubMed]
66. Sae-Tang, W.; Heuvelink, E.; Kohlen, W.; Argyri, E.; Nicole, C.C.S.; Marcelis, L.F.M. Effect of far-red and blue light on rooting in medicinal cannabis cuttings and related changes in endogenous auxin and carbohydrates. *Sci. Hortic.* **2024**, *325*, 112614. [CrossRef]
67. Chen, S.; Marcelis, L.F.M.; Offringa, R.; Kohlen, W.; Heuvelink, E. Far-red light-enhanced apical dominance stimulates flower and fruit abortion in sweet pepper. *Plant Physiol.* **2024**, *195*, 924–939. [CrossRef] [PubMed]
68. Inoue, S.; Kinoshita, T.; Matsumoto, M.; Nakayama, K.I.; Doi, M.; Shimazaki, K. Blue light-induced autophosphorylation of phototropin is a primary step for signaling. *Proc. Natl. Acad. Sci. USA* **2008**, *105*, 5626–5631. [CrossRef]
69. Suetsugu, N.; Wada, M. Evolution of the Cp-Actin-based Motility System of Chloroplasts in Green Plants. *Front. Plant Sci.* **2016**, *7*, 561. [CrossRef] [PubMed]
70. Long, S.P.; Marshall-Colon, A.; Zhu, X.-G. Meeting the Global Food Demand of the Future by Engineering Crop Photosynthesis and Yield Potential. *Cell* **2015**, *161*, 56–66. [CrossRef] [PubMed]
71. Schoepke, T. Cultivo de Marihuana: Manual Básico de Agricultura. 2014. Available online: [https://docs.wixstatic.com/ugd/e7ce82\\_8dff8abf99c4456294a94b71a177bcf0.pdf](https://docs.wixstatic.com/ugd/e7ce82_8dff8abf99c4456294a94b71a177bcf0.pdf) (accessed on 12 April 2025).
72. Bayat, L.; Arab, M.; Aliniaiefard, S.; Seif, M.; Lastochkina, O.; Li, T. Effects of growth under different light spectra on the subsequent high light tolerance in rose plants. *AoB PLANTS* **2018**, *10*, ply052. [CrossRef]
73. Li, T.; Heuvelink, E.; Dueck, T.A.; Janse, J.; Gort, G.; Marcelis, L.F.M. Enhancement of crop photosynthesis by diffuse light: Quantifying the contributing factors. *Ann. Bot.* **2014**, *114*, 145–156. [CrossRef] [PubMed]
74. Islam, M.J.; Ryu, B.R.; Rahman, M.H.; Rana, M.S.; Cheong, E.J.; Wang, M.-H.; Lim, J.-D.; Hossain, M.A.; Lim, Y.-S. Cannabinoid accumulation in hemp depends on ROS generation and interlinked with morpho-physiological acclimation and plasticity under indoor LED environment. *Front. Plant Sci.* **2022**, *13*, 984410. [CrossRef]
75. Jiang, C.; Johkan, M.; Maruo, T.; Hohjo, M.; Tsukagoshi, S.; Ebihara, M.; Nakaminami, A. Effect of supplemental far-red light with blue and red LED lamps on leaf photosynthesis, stomatal regulation and plant development of protected cultivated tomato. *Acta Hortic.* **2018**, *1227*, 533–540. [CrossRef]
76. Liu, J.; Van Iersel, M.W. Far-red Photons Increase Light Capture but Have Lower Photosynthetic Capacity Than Red Photons. *J. Am. Soc. Hortic. Sci.* **2023**, *148*, 253–265. [CrossRef]
77. Jin, W.; Urbina, J.L.; Heuvelink, E.; Marcelis, L.F.M. Adding Far-Red to Red-Blue Light-Emitting Diode Light Promotes Yield of Lettuce at Different Planting Densities. *Front. Plant Sci.* **2021**, *11*, 609977. [CrossRef]
78. Fleischer, W.E. *From the Laboratory of Plan—Physiology*; Cornell University: Ithaca, NY, USA, 1935.
79. Ji, Y.; Ocaña, D.N.; Choe, D.; Larsen, D.H.; Marcelis, L.F.M.; Heuvelink, E. Far-red radiation stimulates dry mass partitioning to fruits by increasing fruit sink strength in tomato. *New Phytol.* **2020**, *228*, 1914–1925. [CrossRef]
80. Pawłowska, B.; Szewczyk-Taranek, B.; Dziedzic, E.; Żupnik, M. Rooting response under LED systems in *Rosa canina* in vitro cultures. *Acta Hortic.* **2017**, *1155*, 519–524. [CrossRef]
81. Christiaens, A.; Gobin, B.; Van Huylenbroeck, J.; Van Labeke, M.-C. Adventitious rooting of Chrysanthemum is stimulated by a low red:far-red ratio. *J. Plant Physiol.* **2019**, *236*, 117–123. [CrossRef] [PubMed]

82. Peçanha, D.A.; Moro Peña, J.Á.; Freitas, M.S.M.; Chourak, Y.; Urrestarazu, M. Effect of light spectra on stem cutting rooting and lavender growth. *Acta Sci. Agron.* **2023**, *45*, e58864. [[CrossRef](#)]
83. Wang, J.-F.; Zhang, T.-L.; Fu, B.-J. A measure of spatial stratified heterogeneity. *Ecol. Indic.* **2016**, *67*, 250–256. [[CrossRef](#)]
84. Lund, J.B.; Blom, T.J.; Aaslyng, J.M. End-of-day Lighting with Different Red/Far-red Ratios Using Light-emitting Diodes Affects Plant Growth of *Chrysanthemum × morifolium* Ramat. ‘Coral Charm.’ *HortScience* **2007**, *42*, 1609–1611. [[CrossRef](#)]
85. Eaves, J.; Eaves, S.; Morphy, C.; Murray, C. The relationship between light intensity, cannabis yields, and profitability. *Agron. J.* **2020**, *112*, 1466–1470. [[CrossRef](#)]
86. Llewellyn, D.; Golem, S.; Foley, E.; Dinka, S.; Jones, A.M.P.; Zheng, Y. Indoor grown cannabis yield increased proportionally with light intensity, but ultraviolet radiation did not affect yield or cannabinoid content. *Front. Plant Sci.* **2022**, *13*, 974018. [[CrossRef](#)]
87. Li, M.; Roman, M.; Yuan, J.; Rehman, M.; Liu, L. Varying light intensity can alter metabolic profile and cannabispirenenone content of industrial hemp. *Ind. Crops Prod.* **2023**, *202*, 117031. [[CrossRef](#)]
88. Mukhopadhyay, P.; Rajesh, M.; Horváth, B.; Bátkai, S.; Park, O.; Tanchian, G.; Gao, R.Y.; Patel, V.; Wink, D.A.; Liaudet, L.; et al. Cannabidiol protects against hepatic ischemia/reperfusion injury by attenuating inflammatory signaling and response, oxidative/nitrative stress, and cell death. *Free Radic. Biol. Med.* **2011**, *50*, 1368–1381. [[CrossRef](#)] [[PubMed](#)]
89. Raja, A.; Ahmadi, S.; De Costa, F.; Li, N.; Kerman, K. Attenuation of Oxidative Stress by Cannabinoids and Cannabis Extracts in Differentiated Neuronal Cells. *Pharmaceuticals* **2020**, *13*, 328. [[CrossRef](#)]
90. Kim, H.-H.; Goins, G.D.; Wheeler, R.M.; Sager, J.C. Green-light Supplementation for Enhanced Lettuce Growth under Red- and Blue-light-emitting Diodes. *HortScience* **2004**, *39*, 1617–1622. [[CrossRef](#)]
91. Piovene, C.; Orsini, F.; Bosi, S.; Sanoubar, R.; Bregola, V.; Dinelli, G.; Gianquinto, G. Optimal red:blue ratio in led lighting for nutraceutical indoor horticulture. *Sci. Hort.* **2015**, *193*, 202–208. [[CrossRef](#)]
92. Jenkins, M.W.; Livesay, C.B. Photosynthetic Performance and Potency of *Cannabis sativa* L. Grown under LED and HPS Illumination. *Agric. Sci.* **2021**, *12*, 293–304. [[CrossRef](#)]
93. Carranza-Ramírez, J.E.; Borda, A.M.; Moreno-Fonseca, L.P. LED light modifies plant architecture, physiological parameters and cannabinoid content in three varieties of *Cannabis sativa* L. *S. Afr. J. Bot.* **2025**, *176*, 231–240. [[CrossRef](#)]
94. Kotiranta, S.; Pihlava, J.-M.; Kotilainen, T.; Palonen, P. The morphology, inflorescence yield, and secondary metabolite accumulation in hemp type *Cannabis sativa* can be influenced by the R:FR ratio or the amount of short wavelength radiation in a spectrum. *Ind. Crops Prod.* **2024**, *208*, 117772. [[CrossRef](#)]
95. Holweg, M.M.S.F.; Kaiser, E.; Kappers, I.F.; Heuvelink, E.; Marcelis, L.F.M. The role of red and white light in optimizing growth and accumulation of plant specialized metabolites at two light intensities in medical cannabis (*Cannabis sativa* L.). *Front. Plant Sci.* **2024**, *15*, 1393803. [[CrossRef](#)]
96. Takeda, F.; Newell, M. A Method for Increasing Fall Flowering in Short-day ‘Carmine’ Strawberry. *HortScience* **2006**, *41*, 480–481. [[CrossRef](#)]
97. Zhen, S.; Bugbee, B. Substituting Far-Red for Traditionally Defined Photosynthetic Photons Results in Equal Canopy Quantum Yield for CO<sub>2</sub> Fixation and Increased Photon Capture During Long-Term Studies: Implications for Re-Defining PAR. *Front. Plant Sci.* **2020**, *11*, 581156. [[CrossRef](#)] [[PubMed](#)]
98. Kotiranta, S.; Sarka, A.; Kotilainen, T.; Palonen, P. Decreasing R:FR ratio in a grow light spectrum increases inflorescence yield but decreases plant specialized metabolite concentrations in *Cannabis sativa*. *Environ. Exp. Bot.* **2025**, *229*, 106059. [[CrossRef](#)]
99. Peterswald, T.J.; Mieog, J.C.; Azman Halimi, R.; Magner, N.J.; Trebilco, A.; Kretzschmar, T.; Purdy, S.J. Moving Away from 12:12; the Effect of Different Photoperiods on Biomass Yield and Cannabinoids in Medicinal Cannabis. *Plants* **2023**, *12*, 1061. [[CrossRef](#)]
100. Chazaux, M.; Schiphorst, C.; Lazzari, G.; Caffarri, S. Precise estimation of chlorophyll *a*, *b* and carotenoid content by deconvolution of the absorption spectrum and new simultaneous equations for Chl determination. *Plant J.* **2022**, *109*, 1630–1648. [[CrossRef](#)]
101. Zhu, X.-G.; Long, S.P.; Ort, D.R. What is the maximum efficiency with which photosynthesis can convert solar energy into biomass? *Curr. Opin. Biotechnol.* **2008**, *19*, 153–159. [[CrossRef](#)] [[PubMed](#)]
102. Merino, J.; Samaniego, I.; López, D.; Viera, W.; Mejía, P.; Jaramillo, P.; Viteri, P.; Gaona, P. Yield and content of cannabidiol (CBD) and tetrahydrocannabinol (THC) in medicinal cannabis (*Cannabis sativa*) grown in the Ecuadorian highlands. *Manglar* **2024**, *21*, 107–113. [[CrossRef](#)]
103. Amrein, P.; Rinner, S.; Pittorino, T.; Espel, J.; Schmidmayr, D. Influence of Light Spectra on the Production of Cannabinoids. *Med. Cannabis Cannabinoids* **2020**, *3*, 103–110. [[CrossRef](#)] [[PubMed](#)]
104. Arora, A.S.; Yun, C.M. Dynamic spectrum lighting impact on plant morphology and cannabinoid profile of medical and recreational cannabis—A novel leapfrog strategy towards shaping the future of horticulture lighting. *Ind. Crops Prod.* **2023**, *199*, 116799. [[CrossRef](#)]
105. Folta, K.M.; Carvalho, S.D. Photoreceptors and Control of Horticultural Plant Traits. *HortScience* **2015**, *50*, 1274–1280. [[CrossRef](#)]
106. Pockock, T. Light-emitting Diodes and the Modulation of Specialty Crops: Light Sensing and Signaling Networks in Plants. *HortScience* **2015**, *50*, 1281–1284. [[CrossRef](#)]

107. Thoma, F.; Somborn-Schulz, A.; Schlehuber, D.; Keuter, V.; Deerberg, G. Effects of Light on Secondary Metabolites in Selected Leafy Greens: A Review. *Front. Plant Sci.* **2020**, *11*, 497. [[CrossRef](#)]
108. Meng, Q.; Boldt, J.; Runkle, E.S. Blue Radiation Interacts with Green Radiation to Influence Growth and Predominantly Controls Quality Attributes of Lettuce. *J. Am. Soc. Hortic. Sci.* **2020**, *145*, 75–87. [[CrossRef](#)]
109. Naznin, M.T.; Lefsrud, M.; Gravel, V.; Azad, M.O.K. Blue Light added with Red LEDs Enhance Growth Characteristics, Pigments Content, and Antioxidant Capacity in Lettuce, Spinach, Kale, Basil, and Sweet Pepper in a Controlled Environment. *Plants* **2019**, *8*, 93. [[CrossRef](#)]
110. Hawley, D.; Graham, T.; Stasiak, M.; Dixon, M. Improving Cannabis Bud Quality and Yield with Subcanopy Lighting. *HortScience* **2018**, *53*, 1593–1599. [[CrossRef](#)]
111. Hall, W.; Stjepanović, D.; Caulkins, J.; Lynskey, M.; Leung, J.; Campbell, G.; Degenhardt, L. Public health implications of legalising the production and sale of cannabis for medicinal and recreational use. *Lancet* **2019**, *394*, 1580–1590. [[CrossRef](#)]
112. Maliakal, S.K.; McDonnell, K.; Dudley, S.A.; Schmitt, J. Effects of Red to Far-Red Ratio and Plant Density on Biomass Allocation and Gas Exchange in *Impatiens capensis*. *Int. J. Plant Sci.* **1999**, *160*, 723–733. [[CrossRef](#)]
113. Kalaitzoglou, P.; Van Ieperen, W.; Harbinson, J.; Van Der Meer, M.; Martinakos, S.; Weerheim, K.; Nicole, C.C.S.; Marcelis, L.F.M. Effects of Continuous or End-of-Day Far-Red Light on Tomato Plant Growth, Morphology, Light Absorption, and Fruit Production. *Front. Plant Sci.* **2019**, *10*, 322. [[CrossRef](#)] [[PubMed](#)]
114. Vincenzi, E.; Ji, Y.; Kerstens, T.; Lai, X.; Deelen, S.; De Beer, E.; Millenaar, F.; Marcelis, L.F.M.; Heuvelink, E. Duration, not timing during the photoperiod, of far-red application determines the yield increase in tomato. *Sci. Hortic.* **2024**, *338*, 113553. [[CrossRef](#)]
115. Sarlikioti, V.; De Visser, P.H.B.; Buck-Sorlin, G.H.; Marcelis, L.F.M. How plant architecture affects light absorption and photosynthesis in tomato: Towards an ideotype for plant architecture using a functional–structural plant model. *Ann. Bot.* **2011**, *108*, 1065–1073. [[CrossRef](#)]
116. Takenaka, A. Effects of leaf blade narrowness and petiole length on the light capture efficiency of a shoot. *Ecol. Res.* **1994**, *9*, 109–114. [[CrossRef](#)]
117. Casal, J.J. Photoreceptor Signaling Networks in Plant Responses to Shade. *Annu. Rev. Plant Biol.* **2013**, *64*, 403–427. [[CrossRef](#)]
118. Landi, M.; Zivcak, M.; Sytar, O.; Brestic, M.; Allakhverdiev, S.I. Plasticity of photosynthetic processes and the accumulation of secondary metabolites in plants in response to monochromatic light environments: A review. *Biochim. Biophys. Acta BBA—Bioenerg.* **2020**, *1861*, 148131. [[CrossRef](#)]
119. Moher, M.; Jones, M.; Zheng, Y. Photoperiodic Response of In Vitro *Cannabis sativa* Plants. *HortScience* **2021**, *56*, 108–113. [[CrossRef](#)]
120. Cervantes, J. *The Cannabis Encyclopedia: The Definitive Guide to Cultivation & Consumption of Medical Marijuana*; Van Patten Publishing: Vancouver, WA, USA, 2015.
121. Dang, M.; Arachchige, N.M.; Campbell, L.G. Optimizing Photoperiod Switch to Maximize Floral Biomass and Cannabinoid Yield in *Cannabis sativa* L. A Meta-Analytic Quantile Regression Approach. *Front. Plant Sci.* **2022**, *12*, 797425. [[CrossRef](#)] [[PubMed](#)]
122. Morello, V.; Brousseau, V.D.; Wu, N.; Wu, B.-S.; MacPherson, S.; Lefsrud, M. Light Quality Impacts Vertical Growth Rate, Phytochemical Yield and Cannabinoid Production Efficiency in *Cannabis sativa*. *Plants* **2022**, *11*, 2982. [[CrossRef](#)]
123. Ahrens, A.; Llewellyn, D.; Zheng, Y. Longer Photoperiod Substantially Increases Indoor-Grown Cannabis' Yield and Quality: A Study of Two High-THC Cultivars Grown under 12 h vs. 13 h Days. *Plants* **2024**, *13*, 433. [[CrossRef](#)]
124. Choi, H.; Back, S.; Kim, G.W.; Lee, K.; Venkatesh, J.; Lee, H.B.; Kwon, J.-K.; Kang, B.-C. Development of a speed breeding protocol with flowering gene investigation in pepper (*Capsicum annuum*). *Front. Plant Sci.* **2023**, *14*, 1151765. [[CrossRef](#)]
125. Gao, C.; Xin, P.; Cheng, C.; Tang, Q.; Chen, P.; Wang, C.; Zang, G.; Zhao, L. Diversity Analysis in *Cannabis sativa* Based on Large-Scale Development of Expressed Sequence Tag-Derived Simple Sequence Repeat Markers. *PLoS ONE* **2014**, *9*, e110638. [[CrossRef](#)]
126. Lynch, R.C.; Vergara, D.; Tittes, S.; White, K.; Schwartz, C.J.; Gibbs, M.J.; Ruthenburg, T.C.; deCesare, K.; Land, D.P.; Kane, N.C. Genomic and Chemical Diversity in *Cannabis*. *Crit. Rev. Plant Sci.* **2016**, *35*, 349–363. [[CrossRef](#)]
127. Sawler, J.; Stout, J.M.; Gardner, K.M.; Hudson, D.; Vidmar, J.; Butler, L.; Page, J.E.; Myles, S. The Genetic Structure of Marijuana and Hemp. *PLoS ONE* **2015**, *10*, e0133292. [[CrossRef](#)]
128. Watson, A.; Ghosh, S.; Williams, M.J.; Cuddy, W.S.; Simmonds, J.; Rey, M.-D.; Asyraf Md Hatta, M.; Hinchliffe, A.; Steed, A.; Reynolds, D.; et al. Speed breeding is a powerful tool to accelerate crop research and breeding. *Nat. Plants* **2018**, *4*, 23–29. [[CrossRef](#)]
129. Schilling, S.; Melzer, R.; Dowling, C.A.; Shi, J.; Muldoon, S.; McCabe, P.F. A protocol for rapid generation cycling (speed breeding) of hemp (*Cannabis sativa*) for research and agriculture. *Plant J.* **2023**, *113*, 437–445. [[CrossRef](#)] [[PubMed](#)]
130. Ghosh, S.; Watson, A.; Gonzalez-Navarro, O.E.; Ramirez-Gonzalez, R.H.; Yanes, L.; Mendoza-Suárez, M.; Simmonds, J.; Wells, R.; Rayner, T.; Green, P.; et al. Speed breeding in growth chambers and glasshouses for crop breeding and model plant research. *Nat. Protoc.* **2018**, *13*, 2944–2963. [[CrossRef](#)]
131. Segrestin, J.; Bernard-Verdier, M.; Violle, C.; Richarte, J.; Navas, M.; Garnier, E. When is the best time to flower and disperse? A comparative analysis of plant reproductive phenology in the Mediterranean. *Funct. Ecol.* **2018**, *32*, 1770–1783. [[CrossRef](#)]

132. Stack, G.M.; Toth, J.A.; Carlson, C.H.; Cala, A.R.; Marrero-González, M.I.; Wilk, R.L.; Gentner, D.R.; Crawford, J.L.; Philippe, G.; Rose, J.K.C.; et al. Season-long characterization of high-cannabinoid hemp (*Cannabis sativa* L.) reveals variation in cannabinoid accumulation, flowering time, and disease resistance. *GCB Bioenergy* **2021**, *13*, 546–561. [[CrossRef](#)]
133. Dong, H.; Clark, L.V.; Jin, X.; Anzoua, K.; Bagmet, L.; Chebukin, P.; Dzyubenko, E.; Dzyubenko, N.; Ghimire, B.K.; Heo, K.; et al. Managing flowering time in Miscanthus and sugarcane to facilitate intra- and intergeneric crosses. *PLoS ONE* **2021**, *16*, e0240390. [[CrossRef](#)] [[PubMed](#)]
134. Stetter, M.G.; Zeitler, L.; Steinhaus, A.; Kroener, K.; Biljecki, M.; Schmid, K.J. Crossing Methods and Cultivation Conditions for Rapid Production of Segregating Populations in Three Grain Amaranth Species. *Front. Plant Sci.* **2016**, *7*, 816. [[CrossRef](#)] [[PubMed](#)]
135. Ferwerda, F.P. Methods to synchronize the flowering time of the components in crossing plots for the production of hybrid seed corn. *Euphytica* **1953**, *2*, 127–134. [[CrossRef](#)]
136. Dowling, C.A.; Shi, J.; Toth, J.A.; Quade, M.A.; Smart, L.B.; McCabe, P.F.; Schilling, S.; Melzer, R. A FLOWERING LOCUS T ortholog is associated with photoperiod-insensitive flowering in hemp (*Cannabis sativa* L.). *Plant J.* **2024**, *119*, 383–403. [[CrossRef](#)]
137. Leckie, K.M.; Sawler, J.; Kapos, P.; MacKenzie, J.O.; Giles, I.; Baynes, K.; Lo, J.; Baute, G.J.; Cledon, J.M. Loss of daylength sensitivity by splice site mutation in Cannabis pseudo-response regulator. *Plant J.* **2024**, *1186*, 2020–2036. [[CrossRef](#)]
138. Singh, D.; Sharma, S.; Jose-Santhi, J.; Kalia, D.; Singh, R.K. Hormones regulate the flowering process in saffron differently depending on the developmental stage. *Front. Plant Sci.* **2023**, *14*, 1107172. [[CrossRef](#)]
139. Burgel, L.; Hartung, J.; Schibano, D.; Graeff-Hönninger, S. Impact of Different Phytohormones on Morphology, Yield and Cannabinoid Content of *Cannabis sativa* L. *Plants* **2020**, *9*, 725. [[CrossRef](#)]
140. Garrido, J.; Rico, S.; Corral, C.; Sánchez, C.; Vidal, N.; Martínez-Quesada, J.J.; Ferreira-Vera, C. Exogenous application of stress-related signaling molecules affect growth and cannabinoid accumulation in medical cannabis (*Cannabis sativa* L.). *Front. Plant Sci.* **2022**, *13*, 1082554. [[CrossRef](#)]
141. Lorensen, M.D.B.B.; Hayat, S.Y.; Wellner, N.; Bjarnholt, N.; Janfelt, C. Leaves of *Cannabis sativa* and their trichomes studied by DESI and MALDI mass spectrometry imaging for their contents of cannabinoids and flavonoids. *Phytochem. Anal.* **2023**, *34*, 269–279. [[CrossRef](#)]
142. Hedden, P.; Sponsel, V. A Century of Gibberellin Research. *J. Plant Growth Regul.* **2015**, *34*, 740–760. [[CrossRef](#)]
143. Plackett, A.R.G.; Wilson, Z.A. Gibberellins and Plant Reproduction. In *Annual Plant Reviews Online*; Roberts, J.A., Ed.; Wiley: Hoboken, NJ, USA, 2017; pp. 323–358.
144. Lee, J.; Oh, M.; Park, H.; Lee, I. SOC1 translocated to the nucleus by interaction with AGL24 directly regulates *LEAFY*. *Plant J.* **2008**, *55*, 832–843. [[CrossRef](#)]
145. Song, Y.H.; Lee, I.; Lee, S.Y.; Imaizumi, T.; Hong, J.C. CONSTANS and ASYMMETRIC LEAVES 1 complex is involved in the induction of *FLOWERING LOCUS T* in photoperiodic flowering in Arabidopsis. *Plant J.* **2012**, *69*, 332–342. [[CrossRef](#)] [[PubMed](#)]
146. Zhu, Y.; Klasfeld, S.; Jeong, C.W.; Jin, R.; Goto, K.; Yamaguchi, N.; Wagner, D. TERMINAL FLOWER 1-FD complex target genes and competition with *FLOWERING LOCUS T*. *Nat. Commun.* **2020**, *11*, 5118. [[CrossRef](#)]
147. Sánchez-Gutiérrez, A.; Narváez-Zapata, J.A.; Salvador-Figueroa, M. Genes Involved in the Transition and Floral Sexual Differentiation of *Jatropha curcas* L. *Plant Mol. Biol. Rep.* **2024**, *42*, 201–217. [[CrossRef](#)]
148. Alter, H.; Sade, Y.; Sood, A.; Carmeli-Weissberg, M.; Shaya, F.; Kamenetsky-Goldstein, R.; Bernstein, N.; Spitzer-Rimon, B. Inflorescence development in female cannabis plants is mediated by photoperiod and gibberellin. *Hortic. Res.* **2024**, *11*, uhae245. [[CrossRef](#)] [[PubMed](#)]
149. Silva, G.F.F.; Silva, E.M.; Correa, J.P.O.; Vicente, M.H.; Jiang, N.; Notini, M.M.; Junior, A.C.; De Jesus, F.A.; Castilho, P.; Carrera, E.; et al. Tomato floral induction and flower development are orchestrated by the interplay between gibberellin and two unrelated micro RNA -controlled modules. *New Phytol.* **2019**, *221*, 1328–1344. [[CrossRef](#)]
150. King, R.W.; Ben-Tal, Y. A Florigenic Effect of Sucrose in *Fuchsia hybrida* Is Blocked by Gibberellin-Induced Assimilate Competition. *Plant Physiol.* **2001**, *125*, 488–496. [[CrossRef](#)]
151. Reinecke, D.M.; Wickramarathna, A.D.; Ozga, J.A.; Kurepin, L.V.; Jin, A.L.; Good, A.G.; Pharis, R.P. Gibberellin 3-oxidase Gene Expression Patterns Influence Gibberellin Biosynthesis, Growth, and Development in Pea. *Plant Physiol.* **2013**, *163*, 929–945. [[CrossRef](#)]
152. Flajšman, M.; Slapnik, M.; Murovec, J. Production of Feminized Seeds of High CBD *Cannabis sativa* L. by Manipulation of Sex Expression and Its Application to Breeding. *Front. Plant Sci.* **2021**, *12*, 718092. [[CrossRef](#)]
153. Baiton, A. Novel Strategies for Sustainable Rapid Breeding of *Cannabis sativa* L. Master's thesis, University of Guelph, Guelph, ON, Canada, 2024.
154. Gruda, N. Impact of Environmental Factors on Product Quality of Greenhouse Vegetables for Fresh Consumption. *Crit. Rev. Plant Sci.* **2005**, *24*, 227–247. [[CrossRef](#)]
155. Summers, H.M.; Sproul, E.; Quinn, J.C. The greenhouse gas emissions of indoor cannabis production in the United States. *Nat. Sustain.* **2021**, *4*, 644–650. [[CrossRef](#)]

156. Namdar, D.; Charuvi, D.; Ajampura, V.; Mazuz, M.; Ion, A.; Kamara, I.; Koltai, H. LED lighting affects the composition and biological activity of *Cannabis sativa* secondary metabolites. *Ind. Crops Prod.* **2019**, *132*, 177–185. [[CrossRef](#)]
157. Roupael, Y.; Cardarelli, M.; Bassal, A.; Leonardi, C.; Giuffrida, F.; Colla, G. Vegetable quality as affected by genetic, agronomic and environmental factors. *J. Food Agric. Environ.* **2012**, *10*, 680–688.
158. Nitz, G.M.; Grubmüller, E.; Schnitzler, W.H. Differential Flavonoid Response to PAR and UV-B Light in Chive (*Allium schoenoprasum* L.). *Acta Hort.* **2004**, *659*, 825–830. [[CrossRef](#)]
159. Bafort, F.; Libault, A.; Maron, E.; Kohnen, S.; Ancion, N.; Jijakli, M.H. Operational Costs and Analysis of Agronomic Characteristics on Cannabidiol and Cannabigerol Hemp (*Cannabis sativa* L.) in Hydroponic Soilless Greenhouse and Field Cultivation. *Horticulturae* **2024**, *10*, 1271. [[CrossRef](#)]
160. García-Tejero, I.F.; Hernández, A.; Ferreiro-Vera, C.; Zuazo, V.H.D.; García, J.H.; Sánchez-Carnerero, C.; Casano, S. Yield of new hemp varieties for medical purposes under semi-arid Mediterranean environment conditions. *Comun. Sci.* **2020**, *11*, e3264. [[CrossRef](#)]
161. Charles, A.P.R.; Gu, Z.; Archer, R.; Auwarter, C.; Hatterman-Valenti, H.; Rao, J.; Chen, B. Effect of High-Tunnel and Open-Field Production on the Yield, Cannabinoids, and Volatile Profiles in Industrial Hemp (*Cannabis sativa* L.) Inflorescence. *J. Agric. Food Chem.* **2024**, *72*, 12975–12987. [[CrossRef](#)]
162. García-Tejero, I.F.; Durán Zuazo, V.H.; Sánchez-Carnerero, C.; Hernández, A.; Ferreiro-Vera, C.; Casano, S. Seeking suitable agronomical practices for industrial hemp (*Cannabis sativa* L.) cultivation for biomedical applications. *Ind. Crops Prod.* **2019**, *139*, 111524. [[CrossRef](#)]
163. Lecholocholo, N.; Shoko, T.; Manhivi, V.E.; Maboko, M.M.; Akinola, S.A.; Sivakumar, D. Influence of different rootstocks on quality and volatile constituents of cantaloupe and honeydew melons (*Cucumis melo* L.) grown in high tunnels. *Food Chem.* **2022**, *393*, 133388. [[CrossRef](#)]
164. Patel, H.; Taghavi, T.; Samtani, J.B. Fruit Quality of Several Strawberry Cultivars during the Harvest Season under High Tunnel and Open Field Environments. *Horticulturae* **2023**, *9*, 1084. [[CrossRef](#)]
165. Jameel, M.M.; Khairie Khesro, M.; Jawad AL-Bayati, H. Effect Traditional Greenhouse (High Tunnel) in the Characteristics of Growth and Yield of the Cucumber. *Plant Arch.* **2021**, *21*, 781–784. [[CrossRef](#)]
166. Zheng, Y.; Llewellyn, D. Lighting and CO<sub>2</sub> in cannabis production. In *Handbook of Cannabis Production in Controlled Environments*; CRC Press: Boca Raton, FL, USA, 2022; pp. 163–188.
167. Caplan, D.; Dixon, M.; Zheng, Y. Optimal Rate of Organic Fertilizer during the Vegetative-stage for Cannabis Grown in Two Coir-based Substrates. *HortScience* **2017**, *52*, 1307–1312. [[CrossRef](#)]
168. Reichel, P.; Munz, S.; Hartung, J.; Kotiranta, S.; Graeff-Hönninger, S. Impacts of Different Light Spectra on CBD, CBDA and Terpene Concentrations in Relation to the Flower Positions of Different *Cannabis sativa* L. Strains. *Plants* **2022**, *11*, 2695. [[CrossRef](#)]
169. Hazekamp, A. An evaluation of the quality of medicinal grade cannabis in the Netherlands. *Cannabinoids* **2006**, *1*, 1–9.
170. Kowal, M.A.; Hazekamp, A.; Grotenhermen, F. Review on clinical studies with cannabis and cannabinoids 2010–2014. *Cannabinoids* **2016**, *11*, 1–18.
171. Burgie, E.S.; Bussell, A.N.; Walker, J.M.; Dubiel, K.; Vierstra, R.D. Crystal structure of the photosensing module from a red/far-red light-absorbing plant phytochrome. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 10179–10184. [[CrossRef](#)] [[PubMed](#)]
172. Galvão, V.C.; Fankhauser, C. Sensing the light environment in plants: Photoreceptors and early signaling steps. *Curr. Opin. Neurobiol.* **2015**, *34*, 46–53. [[CrossRef](#)] [[PubMed](#)]
173. Krahmer, J.; Ganpudi, A.; Abbas, A.; Romanowski, A.; Halliday, K.J. Phytochrome, Carbon Sensing, Metabolism, and Plant Growth Plasticity. *Plant Physiol.* **2018**, *176*, 1039–1048. [[CrossRef](#)]
174. Morrow, R.C. LED Lighting in Horticulture. *HortScience* **2008**, *43*, 1947–1950. [[CrossRef](#)]
175. Mills, E. Energy-intensive indoor cultivation drives the cannabis industry’s expanding carbon footprint. *One Earth* **2025**, *8*, 101179. [[CrossRef](#)]
176. Danziger, N.; Bernstein, N. Too Dense or Not Too Dense: Higher Planting Density Reduces Cannabinoid Uniformity but Increases Yield/Area in Drug-Type Medical Cannabis. *Front. Plant Sci.* **2022**, *13*, 713481. [[CrossRef](#)]
177. Benevenuto, S.d.S.; Freeman, J.H.; Yang, R. How do pinching and plant density affect industrial hemp produced for cannabinoids in open field conditions? *Agron. J.* **2021**, *114*, 618–626. [[CrossRef](#)]
178. Feeney, M.; Punja, Z.K. Tissue culture and Agrobacterium-mediated transformation of hemp (*Cannabis sativa* L.). *Vitr. Cell. Dev. Biol.-Plant* **2003**, *39*, 578–585. [[CrossRef](#)]
179. Lata, H.; Chandra, S.; Khan, I.; ElSohly, M.A. Thidiazuron-induced high-frequency direct shoot organogenesis of *Cannabis sativa* L. *Vitr. Cell. Dev. Biol.-Plant* **2009**, *45*, 12–19. [[CrossRef](#)]
180. Piuanno, K.F.; Golenia, G.; Boudko, E.A.; Downey, C.; Jones, A.M.P. Regeneration of shoots from immature and mature inflorescences of *Cannabis sativa*. *Can. J. Plant Sci.* **2019**, *99*, 556–559. [[CrossRef](#)]
181. Mobini, S.H.; Lulsdorf, M.; Warkentin, T.D.; Vandenberg, A. Plant growth regulators improve in vitro flowering and rapid generation advancement in lentil and faba bean. *Vitr. Cell. Dev. Biol.-Plant* **2015**, *51*, 71–79. [[CrossRef](#)]

182. Adams, S.R.; Valdés, V.M.; Fuller, D. The effects of day and night temperature on *Chrysanthemum morifolium*: Investigating the safe limits for temperature integration. *J. Hortic. Sci. Biotechnol.* **2009**, *84*, 604–608. [[CrossRef](#)]
183. Hall, J.; Bhattarai, S.P.; Midmore, D.J. The Effects of Photoperiod on Phenological Development and Yields of Industrial Hemp. *J. Nat. Fibers* **2014**, *11*, 87–106. [[CrossRef](#)]
184. Croser, J.S.; Pazos-Navarro, M.; Bennett, R.G.; Tschirren, S.; Edwards, K.; Erskine, W.; Creasy, R.; Ribalta, F.M. Time to flowering of temperate pulses in vivo and generation turnover in vivo–in vitro of narrow-leaf lupin accelerated by low red to far-red ratio and high intensity in the far-red region. *Plant Cell Tissue Organ Cult.* **2016**, *127*, 591–599. [[CrossRef](#)]

**Disclaimer/Publisher’s Note:** The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.