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SPECTRAL ENGINEERING OF PLANT METABOLISM IN CONTROLLED ENVIRONMENT AGRICULTURE: MECHANISMS, METABOLIC REPROGRAMMING, AND PRECISION LIGHTING STRATEGIES

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ABSTRACT
Controlled environment agriculture (CEA) is a promising solution to sustainable crop production under growing pressure from climate change, urbanisation and resource constraints. One of the key technological advances in CEA is the application of spectral engineering with programmable light-emitting diode (LED) systems to precisely control plant growth, metabolism, morphology and nutritional quality. The present review critically evaluates the role of spectral environments in modulating plant physiological and biochemical processes with special emphasis on photosynthesis, carbon and nitrogen metabolism, antioxidant responses, secondary metabolite biosynthesis and crop-specific quality parameters. The review discusses the use of dynamic lighting strategies, spectral-spatial optimisation and pre-harvest illumination approaches to boost productivity and phytochemical accumulation in horticultural crops and recent advances in integrating metabolomics, transcriptomics, high-throughput phenotyping, artificial intelligence, deep learning, and digital twin technologies in the context of intelligent environmental control and predictive cultivation systems. Furthermore, current challenges regarding energy consumption, economic feasibility, reproducibility and large-scale implementation of plant factory systems with artificial lighting are critically analysed. The results show that effective spectral engineering demands crop and growth stage specific spectral recipes, rather than universal ones. Further integration of photobiology, computational modelling, smart sensing systems and sustainable energy management will be key to future progress in CEA and to generate adaptive cultivation systems that can improve yield, nutritional quality, stress resilience and resource-use efficiency concurrently. In brief, spectral engineering is a developing multidisciplinary field with great promise for advancing sustainable and intelligent indoor agriculture.

KEYWORDS
Artificial intelligence in agriculture; Controlled environment agriculture; Plant factory with artificial lighting (PFAL); Plant metabolism; Spectral engineering

INTRODUCTION

Climate instability, urbanisation, decreasing arable land and increasing demand for sustainable food production systems present great challenges for global agriculture. These pressures have led to the rapid development of controlled environment agriculture (CEA), such as vertical farms, hydroponics, smart greenhouses and plant factories with artificial lighting (PFALs), where environmental parameters can be precisely controlled to achieve maximum productivity and crop quality (1,2). Compared to traditional cultivation systems, CEA allows for year-round production, while improving resource-use efficiency, reducing water consumption, minimising pesticide dependency, and enabling localised food production in urban environments (3,4).

Among environmental factors, light is the main regulator of plant growth and metabolism as an energy source for photosynthesis and a developmental signal. Plants sense changes in spectral quality, intensity, duration and direction by photoreceptors including phytochromes, cryptochromes, phototropins, and UV RESISTANCE LOCUS 8 (UVR 8) that regulate photo morphogenesis, circadian rhythms, nutrient assimilation, stress responses and secondary metabolite biosynthesis (5,6). Thus, the spectral environment is of great importance for biomass accumulation, nutritional quality, and environmental adaptation.

The rapid development of light-emitting diodes (LED) technologies has revolutionised modern indoor horticulture by allowing programmable control of spectral composition, light intensity and photoperiod. Compared with traditional lighting systems, LEDs have high energy efficiency, low thermal radiation, spectral specificity, and flexible wavelength combinations that can be optimised for specific crops (7,8). The benefits have turned spectral engineering into a precision cultivation strategy that controls photosynthesis, nutrient metabolism, flowering, stress tolerance and phytochemical accumulation by deliberate modification of light quality.

Recent studies have revealed that spectral regulation not only involved in morphological control, but also directly affects transcriptional, metabolomic and physiological pathways related to primary and secondary metabolism . Blue and UV wavelengths generally stimulate the metabolism of antioxidants and biosynthesis of phenyl propanoids, while red and far-red wavelengths have a strong influence on carbon allocation, canopy architecture, and flowering responses (9–11). Furthermore, the integration of multi-omics technologies, high-throughput phenotyping, and artificial intelligence-assisted environmental control systems are enabling the predictive optimisation of crop metabolism and resource-use efficiency in indoor farming systems (12,13).

Significant advances have been made, but knowledge about spectral engineering remains fragmented across plant physiology, photobiology, metabolic regulation and environmental engineering. Many studies focus on individual wavelengths or single-crop responses, whereas integrated understanding of dynamic spectral interactions, genotype-dependent responses, energy optimisation, and AI-assisted lighting management is still limited. The experimental design, spectral protocols and cultivation conditions are inconsistent further complicating a comparative interpretation among studies.

Therefore, this review presents a system level synthesis of recent advances in spectral engineering of plant metabolism in controlled environment agriculture. Special emphasis is given to photoreceptor-mediated signalling, spectral regulation of plant physiology and metabolism, dynamic lighting strategies, omics-assisted metabolic reprogramming, and intelligent environmental control systems. The paper also critically reviews current challenges, technological limitations and future opportunities for precision spectral management in sustainable horticultural production.

Fundamentals of Plant Light Perception and Signal Transduction

Plants have highly sophisticated light sensing systems that respond to spectral, temporal and spatial changes in the environment and convert them into coordinated physiological and metabolic responses. These responses are controlled by specialised photoreceptors that regulate photomorphogenesis, photosynthesis, circadian rhythms, stress acclimation, and developmental transitions (14,15). Such signalling networks allow plants to continuously adapt growth and metabolism to the changing light environments that they experience in natural and controlled cultivation systems.

Phytochromes (PHYs) are mainly involved in the perception of red and far-red light and control seed germination, shade avoidance, chloroplast development and flowering induction. These photoreceptors have two interconvertible forms, Pr and Pfr, which enable plants to sense changes in red:far-red ratios associated with canopy shading and planting density. Activation of phytochrome modulates carbon allocation, leaf expansion and canopy architecture by inhibiting elongation growth through degradation of PHYTOCHROME-INTERACTING FACTORS (PIFs) (15,16). Hence, far-red enrichment in dense canopies induces shade-avoidance responses that include stem elongation and biomass partitioning changes.

Blue-light responses are primarily mediated by cryptochromes (CRYs) and phototropins (PHOTs), which regulate stomatal opening, chloroplast movement, phototropism, circadian entrainment and antioxidant metabolism. Cryptochrome signalling affects transcription factors involved in flavonoid biosynthesis and stress response, while phototropins improve photosynthetic efficiency by relocating chloroplasts and regulating stomatal function (17,18). Blue light mediated signalling also plays a role in the compact morphology, chlorophyll stability and increased photoprotection often observed in indoor cultivation systems with blue wavelength supplementation.

Perception of ultraviolet-B radiation is mainly through a dedicated photoreceptor, UV RESISTANCE LOCUS 8 (UVR8), which functions in photoprotection and stress signalling. UVR 8 activation stimulates antioxidant defence pathways and enhances biosynthesis of phenolic compounds, flavonoids and anthocyanins that function as protective metabolites to oxidative stress and radiation damage (9,19). Therefore, controlled UV-B supplementation in horticultural crops generally increases the accumulation of phytochemicals and antioxidant capacity, but excessive exposure may damage the stability of photosynthesis and cellular integrity.

Light perception seems to funnel into rather complex downstream signalling networks, with ELONGATED HYPOCOTYL 5 (HY5) and CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) taking the lead. There are also circadian regulators and various hormone–linked transcription factors involved too, giving it a high degree of complexity. In low light, or outright darkness, COP 1 tends to rein in photomorphogenesis, mainly by driving the breakdown of positive light-responsive regulators. Then, when light shows up, COP 1 activity gets inhibited and HY5 is kept stable, so genes connected with photosynthesis, nitrogen metabolism ,chloroplast differentiation and the formation of secondary metabolites are enabled (17,20). Furthermore, these pathways intersect with auxin, gibberellin, brassinosteroid, and jasmonic acid signalling networks. Spectral sensing is not merely an isolated sensory input; rather, it is intrinsically coupled with developmental pathways and metabolic control through a downstream, tightly coordinated regulatory network that dynamically tunes physiological states.

Recent evidence also suggests there are wide-ranging interactions between photoreceptor signalling and circadian control. Different spectral surroundings can shift circadian clock related genes, and those genes in turn help align photosynthetic performance, carbohydrate processing, flowering outcomes, and stress coping, all in step with everyday light cycles. In dynamic lighting experiments inside controlled environment agriculture, researchers report that time based spectral tuning can really change photo system steadiness, cyclic electron transport and metabolic acclimation when plants are kept under longer photoperiods (21). Overall, these results point to how

important it is to blend photobiology together with circadian regulation, especially when we design precision spectral management strategies.
Collectively, photoreceptor mediated signalling networks function as central regulatory systems, linking what the plant perceives in environmental light with growth, metabolism, and stress adaptation. With the new programmable LED technologies, we can now manipulate these pathways with more accuracy, which makes spectral engineering a key framework for better metabolic optimization and even more “intelligent” crop management in modern controlled environment agriculture systems. The effects of different light spectra on plant growth, physiological processes, and metabolic regulation are illustrated in **Fig. 1**.

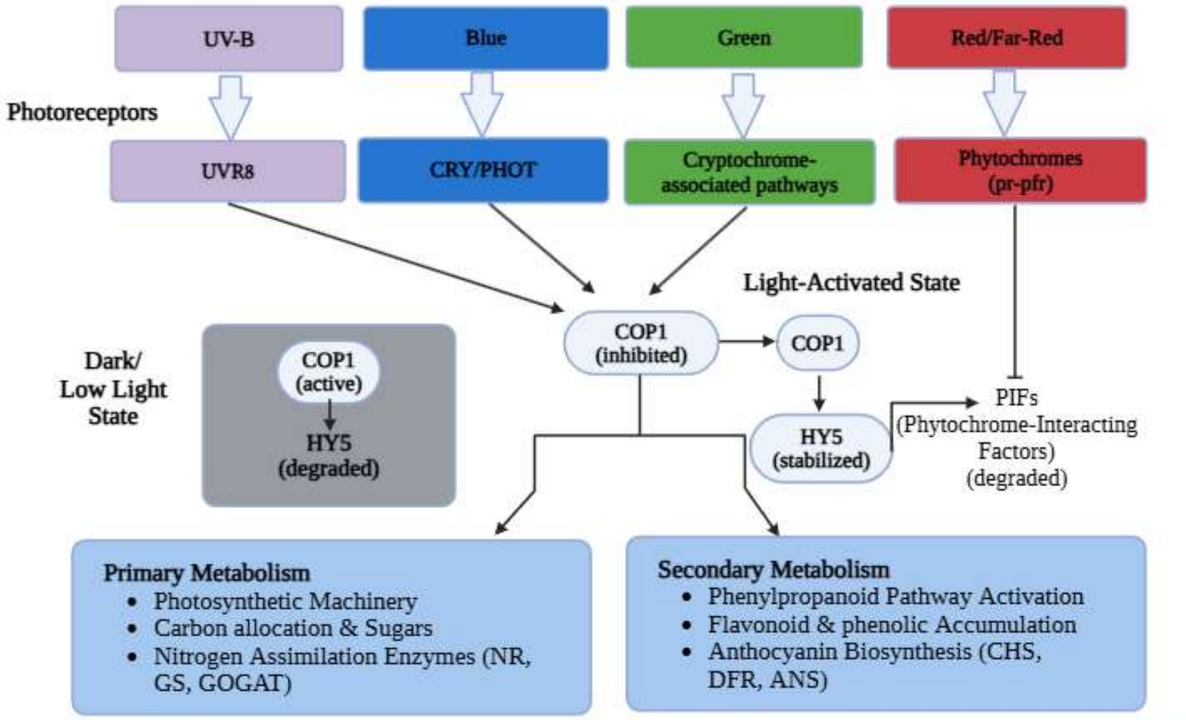

Figure 1. Schematic representation of wavelength-specific LED light spectra by plant photoreceptors and their downstream signaling pathways. Cryptochromes and phototropins perceive blue light, phytochromes perceive red/far-red light, and UVR8 senses UV-B, together they regulate transcriptional networks that control plant growth, development, photosynthesis, metabolism, and stress adaptation.

Spectral Regulation of Plant Physiology
Light quality actually has profound effects on plant physiology, by driving photosynthesis, stomatal conductance, transpiration, morphogenesis, flowering, and stress adaptation all together. In controlled environment agriculture (CEA), it is possible to tweak the spectral composition using programmable LED systems so they gain more exact control over physiological behaviour and eventual crop quality, in line with species specific production aims (22,23). So these controlled spectral settings don’t simply act as a light source, but more like a regulatory instrument, one that can reshape plant structure, overall productivity and metabolic stability at the same time.
Red wavelengths exert a profound influence on photosynthetic carbon assimilation. This happens mainly because chlorophyll pigments gobble them up quite efficiently and also because they are directly tied to photo system II function. In many cases, when the environment gets redder, we often see faster biomass accumulation, wider leaf expansion, and more canopy development, especially in the vegetative growth window (24,25). If red-light is too dominant, plant traits can shift the other way, with more elongated form, lower stomatal conductance, and weaker photo protection that seems to come from unbalanced photoreceptor signalling plus changed chloroplast performance. So, monochromatic red-light setups are usually not the best, for long-term crop production inside controlled indoor systems.
Blue light has a crucial role in stomatal regulation, chloroplast differentiation, phototropism, and also in photo protection. When the blue light fraction goes up, it generally pushes a more compact look, better chlorophyll stability, and higher antioxidant performance, driven by signalling from cryptochrome and becomes phototropin , in other words via pathway mechanisms (26,27). In celery and basil cultivation setups, giving extra blue light really boosts flavonoid build up, makes leaves look more vivid, and keeps photosynthesis steadier, while also reducing unwanted stem elongation. Blue-light exposure, in addition, helps with stomatal opening and improves transpiration efficiency, so nutrient transport and the water-use rhythm in hydroponic systems being affected.
Green wavelengths, which used to be seen as physiologically less important, now, appear to contribute a lot to canopy level photosynthesis and how radiation actually goes through the plant cover. Since green light tends to move further into thick canopies than the red or blue parts, it may boost photosynthesis efficiency in the lower

canopy, and at the same time improve how evenly light is distributed across leaves, especially in multilayer growing systems. In other words, this can make the whole setup act more uniform, not just brighter (28,29). Green-light addition has also been linked with changes in nitrate assimilation, along with chloroplast acclimation responses when plants are kept under controlled lighting setups, so it seems to play wider role. Far red radiation tends to regulate shade avoidance responses, biomass partitioning, and flowering induction through modulating phytochrome photoequilibrium. Additional far red wavelengths often help with canopy expansion and boost radiation interception efficiency, especially in dense vertical farming systems, where the light in the lower canopy becomes limiting. (30). However, excessive enrichment of far-red radiation can result in a reduction of leaf thickness, antioxidant concentration, and overall plant compactness, as carbon allocation patterns shift toward shade acclimation responses.

Ultraviolet radiation works mainly like a regulatory stress flag that nudges photoprotective plus antioxidant responses to switch on. In many cases, a careful UV-A and UV-B addition can improve build up of flavonoids, phenolics, and a bunch of other ROS scavenging compounds, tied to stress acclimation and also to nutritional quality (10,31). Prolonged exposure to ultraviolet radiation can compromise photosynthetic efficiency and induce oxidative stress, particularly when the irradiance intensity exceeds the capacity of endogenous antioxidant scavenging networks.

Plant physiological reactions to spectral environments are also shaped by the photoperiod, the genotype, where the plant is at development, nutrient supply, and all those kinds of environmental interactions that get mixed together. So even if the lighting looks “identical” on paper, it can still end up giving pretty different results between crops and cultivars. New dynamic lighting work also suggests that changing the spectrum over time can help plants adjust their photosynthesis better, use energy more efficiently, and handle stress more calmly, even in continuous or long photoperiod setups (21,32). Collectively, these findings underscore the critical importance of crop-specific spectral optimization within contemporary controlled-environment agriculture (CEA).

Overall, spectral regulation in plant physiology involves highly interwoven interactions among photosynthesis, photoreceptor signalling, environmental adaptation, and metabolic governing. In recent years, advances in programmable lighting technologies are now increasingly enabling very precise physiological adjustments, and in turn, it makes spectral engineering feel like a main tactic for boosting productivity, improving resource-use efficiency, and refining crop quality within controlled environment agriculture systems.

Spectral Engineering of Primary Metabolism

Primary metabolism links light captures with carbon fixation, carbohydrate routing, nitrogen assimilation, mineral nutrition and the whole cellular energy balance. In controlled environment agriculture, spectral tweaking can therefore steer not only biomass output but also the efficiency by which plants convert light and nutrients into edible yield. Photosynthesis still stays the main entry point for this control, because spectral quality influences chlorophyll excitation, electron transport, stomatal conductance, and downstream carbon metabolism. The wider photosynthetic basis for light-driven ATP and reducing-power generation is basically the biochemical groundwork behind these responses (33).

Carbon assimilation and sugar metabolism are really influenced by light quality, the intensity, and the photoperiod. (34) showed that light not only steers starch formation, sucrose synthesis, cell wall composition, vascular development, and also sugar-related gene expression, so the spectral influence goes further than photosynthesis, and it keeps shaping carbon distribution, structural building. If we keep the conditions controlled, then this implies that “spectral recipes” can redirect the assimilated carbon toward leaf expansion, storage carbohydrates, secondary metabolism, or even stress acclimation, depending on the crop stage, and the specific wavelength mix.

Nitrogen assimilation is another big target of spectral engineering, because nitrate reduction and amino acid synthesis need both photosynthetic energy and carbon skeletons. In spinach, (35) showed that adding green light, under nitrogen limitation, helped to raise chlorophyll build-up and strengthened electron transport as well as the performance of nitrogen- assimilatory enzymes , including nitrate reductase, glutamine synthetase, glutamate synthase, and glutamate dehydrogenase. That result backs the idea that green light isn’t only a wavelength that slips through the canopy, but it can also take part in carbon–nitrogen coordination when nutrients are under stress.

Spectral regulation of mineral nutrition matters a lot in hydroponic and vertical farming setups, where nutrient delivery is pretty much tightly guided. (36) brought together evidence that LED spectral management, especially red-to-blue balance, affects how selenium is taken up, how it moves within plant tissues, nitrate metabolism, antioxidant activity, and even phenolic accumulation in CEA crops. In their review they also point out a main bottleneck, in that many light and nutrient studies still feel hard to compare, because selenium dose, nutrient species, light intensity, photoperiod, and the crop genotype are seldom standardized, all at once.

Primary metabolism is tightly connected with redox regulation. Like blue, UV, and high intensity light can push excitation pressure up and make ROS form, yet if the spectral balance is appropriate it can switch on antioxidant systems while not triggering too much oxidative harm. In celery, adding moderate supplemental blue light seemed to boost chlorophyll buildup, raise PS II quantum efficiency, lift the net photosynthetic rate, enhance antioxidant enzyme activity, and improve source–sink performance, but when the spectral balance got skewed it also brought the risk of lowering physiological efficiency (26). These organ specific reactions suggest that primary metabolism really should be checked at the whole plant scale rather than only by looking at leaf photosynthetic traits.

Advancements in metabolomics continue to clarify how variations in the light spectrum reprogram metabolic fluxes at the intersection of primary and secondary pathways. (37) used metabolomic profiling in Brassica microgreens, and they show that LED spectra plus nutrient conditions changed phytochemical composition. In other words, spectral control can redirect metabolic networks, not only bump up growth. Likewise, selenium LED interactions and pre harvest environmental treatments hint that nutrient metabolism, antioxidant regulation, and carbon allocation need to be optimized together, rather than being handled as separate management factors.

Overall, spectral engineering of primary metabolism kind involves a coordinated regulation of photosynthesis, carbohydrate partitioning, nitrogen assimilation, mineral uptake, and redox balance. The strongest future direction doesn't feel like it's a single universal "best spectrum", but more like crop and growth-stage specific integration of light recipes with nutrient management, photoperiod control and metabolic profiling. This kind of integrated strategy is essential for making yield stability better, improving nutrient-use efficiency, and also boosting nutritional quality in controlled environment agriculture. The physiological and metabolic effects of different light spectra in controlled environment agriculture are summarized in **Table 1**.

Table 1. Physiological and Metabolic Effects of Different Spectral Wavelengths in Controlled Environment Agriculture

Spectral Region	**Major Photoreceptors**	**Primary Physiological Responses**	**Major Metabolic / Quality Responses**	**Reference**
Red light	Phytochromes	Enhanced photosynthesis, biomass accumulation, leaf expansion	Increased carbohydrate accumulation and growth efficiency	(28,30)
Blue light	Cryptochromes, phototropins	Stomatal regulation, chlorophyll synthesis, improved photosynthetic efficiency	Enhanced flavonoids, antioxidants, anthocyanins, and stress tolerance	(28,49)
Green light	Cryptochrome-associated signalling	Canopy penetration and lower-leaf photosynthesis	Improved nitrogen assimilation and canopy-level productivity	(5,28,29,35)
Far-red light	Phytochromes	Shade-avoidance signalling, stem elongation, canopy expansion	Altered carbon allocation and developmental regulation	(5,30)
UV-A / UV-B	UVR 8 and stress-signaling pathways	Stress acclimation and photoprotection	Increased flavonoids, phenolics, anthocyanins, and antioxidant metabolism	(14,25,41)

Spectral Regulation of Secondary Metabolism and Nutraceutical Quality

Secondary metabolites play essential roles in plant defences, photo protection, environmental adaption and crop quality. In horticultural crops, those compounds like flavonoids, anthocyanins, carotenoids, terpenoids, phenolic acids, and volatile organic compounds also known as VOCs, can strongly shape the nutritional value, antioxidant strength, the pigmentation, aroma and flavour plus even some pharmaceutical potential. Since a lot of these pathways are very responsive to light, spectral engineering has turned into an important strategy for improving nutraceutical quality in controlled environment agriculture,(9,38).

Flavonoid and phenolic metabolism are quite sensitive to the spectral composition as well as the light intensity. In celery, (39) showed that when the light intensity was moderate, there was a clear rise in total flavones and phenolics, also vitamin C , and the apigenin buildup. At the same time the activities of phenylpropanoid related enzymes went up like PAL, CHS, CHI, and FNS. When the light intensity was pushed higher, anthocyanin accumulation kept increasing too, which suggests that the different flavonoid branches are not governed in exactly the same way depending on the irradiance. Overall, these results support the idea that spectral settings regulate secondary metabolism via both transcriptional regulation and enzyme level control, like a double pathway effect.

Anthocyanin biosynthesis is fairly tied to wavelength, the developmental stage, and genotype all at once. In strawberry, (11) said light quality regulates expression of structural genes like CHS, DFR, ANS, and UFGT, along with transcriptional regulators such as FaMYB10 and FaHY5, which in turn coordinate pigment biosynthesis while the fruit ripens. Still, responses to blue light are not always consistent from one stage to the next. (40) pointed out that blue-light exposure can, either boost anthocyanin buildup or tone it down, depending on when the treatment is started, whether the material is already postharvest, and how sensitive a given cultivar's metabolism. Put together, these differences suggest the need for stage-specific spectral management, instead of leaning on generalized wavelength recommendations only.

Ultraviolet radiation works more like a metabolic elicitor than it does a genuine photosynthetic driver. When UV-B or UV-C is used, exposure often triggers antioxidant and defense linked pathways, which then drive up the build up of flavonoids, anthocyanins, phenolic acids, alkaloids, and terpenoids. In strawberry tissues, UV-C treatment seemed to push epidermal anthocyanin higher via oxidative stress related signalling responses (11). Also in studies on medicinal plants, controlled UV treatment can nudge the biosynthesis of pharmaceutically relevant secondary metabolites, but the outcome stays very tied to species, and dosage too (41). Still, too much UV can end up hurting photosynthetic performance and even cellular stability if the antioxidant shield is not enough, or not fast enough.

Spectral regulation also strongly influences carotenoid accumulation and antioxidant metabolism. In celery leaves, a suitable light intensity improved carotenoid concentration and chlorophyll stability, plus boosted antioxidant enzyme activity; whereas too much or too little irradiance reduced the overall physiological quality (39). Similar kinds of trends have been found in leafy vegetables and microgreens where blue-enriched or mixed red–blue spectra enhanced antioxidant activity, and increased phytochemical accumulation, through higher excitation pressure and ROS-related signalling pathways. These responses show how tightly secondary metabolism connects to photoprotective stress acclimation, and how they go hand in hand in practice.

Volatile compounds and aroma-linked metabolites are also really reactive to the way the spectra are set up, under different lighting conditions. In basil, (42) reported that narrowband blue as well red LED treatments changed the volatile organic compound profiles, which are tied to flavor quality and even commercial acceptability. After that, other basil work has again made it clear that messing with the light spectrum influences morphology, coloration, chlorophyll fluorescence, and postharvest quality traits, and in the same time it also shifts volatile metabolism (27). Taken together these results suggest that spectral engineering can regulate both sensory quality and phytochemical makeup at once, in culinary herbs, as well as in specialty crops.

Pre harvest spectral treatments have showed up as useful approaches for improving nutraceutical quality like right before harvest. (43) said that targeted pre harvest illumination in hydroponic lettuce cut down nitrate build up, but also boosted phenolic content and antioxidant capacity. Those short lasting treatments are commercially attractive because they upgrade functional quality without causing big long term growth troubles or demanding too much energy. The integration of spectral engineering with omics technologies, artificial intelligence, and precision controlled-environment agriculture is summarized in **Fig. 2**. **Dynamic Lighting Strategies and Precision Spectral Management**

Advances in programmable LED tech have allowed this shift, from fairly static lighting arrangements to more lively spectral management approaches that can tune plant growth and metabolism in step with growth phase, physiological conditions, and the actual production targets. In contrast with fixed spectrum lamps, these dynamic setups can read just the spectral mix, the light strength, and even the day length timing in real time, and that tends to boost photosynthetic efficiency , which can also raise crop quality while supporting better energy use inside CEA systems (44,45).

Stage specific spectral management is getting used more and more to tune crop output across the various developmental phases. Usually, red enriched spectra are fed during the vegetative phase, to help the canopy spread out and build more biomass, while later on higher blue light portions are used to push tighter growth habit, keep chlorophyll levels longer, support antioxidant metabolism, and raise overall visual quality. In basil and leafy vegetables, dynamic spectral shifting changed plant form, pigmentation, volatile profile, and postharvest performance, showing pretty clearly that spectral effects depend on where the plant is in its development (27,42).

Pre-harvest illumination strategies have showed up as fairly efficient ways for boosting nutritional quality without really cutting yield too much. Short periods of exposure to blue, UV-A, or even mixed spectral treatments before harvest often boost antioxidant activity, build up phenolic compounds, improve coloration, and also lift sensory quality. In hydroponic lettuce , (43) showed that messing with the lighting before harvest led to lower nitrate levels , while the total phenolic content and antioxidant capacity went up. These kinds of approaches are commercially attractive, mainly because they raise functional quality but keep the long term energy demand comparatively low.

Continuous-light cultivation systems are, another big place where we try to tune the spectrum in indoor agriculture. When the photoperiod is longer, you get a higher daily light integral and often it helps plants build more biomass. But, if the plants stay under light for too long, some species can start showing chlorosis and oxidative imbalance, carbohydrate imbalance, and even photosystem instability. (21) said that using alternating blue and far-red spectral regimes helps plants get used to continuous light. They tied this to cyclic electron transport control, PS II stability, and circadian synchronization in tomato and mini-cucumber setups. In a similar way, (32) found that laser diode-based lighting gave better photosynthetic performance and less thermal stress than standard LEDs when they ran extended photoperiod cultivation. Overall, these results suggest that a well-timed spectral schedule, not just a constant spectrum, can reduce the physiological problems that come with prolonged illumination.

Far-red integration is slowly getting more attention as one key part in dynamic lighting systems, mainly because of what it does to canopy layout and how much radiation actually gets caught. When we add supplemental far-red, the leaves tend to expand and lower-canopy light goes further, especially in multilayer vertical farming setups, where self shading causes a kind of uneven photosynthesis. Still, if far-red is pushed too far it can backfire: plants may become less compact and phytochemical levels can drop, likely due to shade avoidance and the way carbon

gets allocated. So, choosing the right red, blue, far-red mix remains complicated, since crop genotype and the production target both are important for optimal output.
Recent engineering advances have additionally leaned into spectral spatial optimization, and more adaptive light distribution in the field too. (45) showed that spatial optimization models can improve photon distribution uniformity, and also cut down energy waste within plant factory systems. They performed by tweaking spectral delivery based on canopy geometry together with cultivation density. In a similar direction, (44) put forward lighting set ups that follow a Gaussian distribution for micro green cultivation. Their system helped to increase light-use efficiency, while still preserving biomass productivity, and the phytochemical quality. Taken together, these directions suggest a stronger coupling between plant physiology and engineering optimization, as next generation CEA systems keep moving forward.
Energy consumption is still one of the main constraints for commercial indoor farming. In vertical farms and PFAL setups, artificial lighting basically adds a lot to the operating costs, so there is a stress on the importance of crop specific light recipes, plus intermittent lighting approaches, and also "smart" environmental control setups that boost growth with low electricity usage (12,46). These kinds of methods are likely to be instrumental for both the financial viability and the environmental sustainability when indoor agriculture scales up.
More specifically, dynamic lighting strategies feel like a move away from fixed, steady illumination toward a more responsive style of environmental regulation, where plant physiology and metabolism are treated alongside energy management. With ongoing improvements in programmable LEDs, adaptive spectral scheduling, and engineering optimization, the field should keep getting better at precision horticulture as well as more metabolically guided crop production, all within controlled environment agriculture.

Integration of Omics Technologies, High-Throughput Phenotyping, and Artificial Intelligence in Spectral Engineering
The increasing complexity of controlled environment agriculture (CEA) systems has really sped up the integration of omics tools, high throughput phenotyping, and artificial intelligence (AI) into spectral engineering research, all at once. Back when people relied only on traditional physiological measurements, it often felt like it couldn't really untangle how spectral environments, in a linked way, influence metabolism, stress acclimation, development, and ultimately crop quality. So naturally, transcriptomics, metabolomics, proteomics, ionomics, and phenomics are being used together more and more, to map how plants respond to programmable lighting systems, at a systems-biology level (13). Recent studies demonstrating crop-specific responses to spectral engineering are summarized in **Table 2**.

Table 2. Emerging Technologies in Smart Controlled Environment Agriculture Systems

Technology	Application in CEA	Major Advantage	Reference
Artificial intelligence	Predictive environmental control	Improved cultivation precision	(13,15)
Deep learning	Crop monitoring and stress detection	Automated decision-making	(13,20)
Digital twins	Virtual simulation of cultivation systems	Real-time optimization	(52,53)
High-throughput phenotyping	Non-destructive crop assessment	Rapid physiological analysis	(54)
Hyper spectral imaging	Stress and pigment detection	Early diagnosis and monitoring	(54)

Transcriptomic studies indicate that spectral quality somehow controls expression of genes tied to photosynthesis, circadian timing, ROS detoxification, nutrient metabolism, and even the making of secondary metabolites. In leafy vegetables, it has been reported that light quality can change the expression of both structural and regulatory genes in anthocyanin and flavonoid pathways, so it looks like spectral regulation works via a coordinated transcriptional reprogramming, not just some isolated metabolic consequence (20,47). On top of that, spectral environments also seem to interface with hormone associated signalling routes, which are connected with developmental plasticity and environmental acclimation.
Epigenetic regulation is emerging as another key piece of long- term spectral responses. In particular, (48) reported that blue and UV-A irradiation, modified histone associated regulation and transcript buildup connected to carotenoid and theanine biosynthesis in tea plants (Camellia sinensis). So, these outcomes mean that programmable light surroundings do more than drive quick metabolic adjustments, they can also steer longer adaptive developmental regulation.
Metabolomic work adds more evidence that spectral environments reshape biochemical pathways, plus they affect how nutrients get allocated. For Brassica microgreens, (37) found that LED spectral treatments, significantly changed phytochemical composition and metabolites that link to antioxidant activity. In a similar way, (49) reported great differences in antioxidant metabolism and phytochemical accumulation, across distinct spectral

environments. Taken together, these studies point at how useful metabolomics can be for catching crop specific spectral responses and for building targeted phytochemical boosting strategies.

High throughput phenotyping tech is being stitched more and more with spectral engineering, so we can do fast, non-destructive checks on crop performance. Things like chlorophyll fluorescence imaging, hyperspectral sensing, and thermal imaging, plus canopy reflectance analysis help to track in near real time, photosynthetic efficiency, stress behaviours, pigment building up and also canopy unevenness when the lighting changes during the day or at least across the scan. This is really crucial for multilayer vertical farming setups, because light has to travel down through layers, canopy penetration matters a lot and the way spatial light is distributed ends up shaping not just yield, but metabolic uniformity as well.

Artificial intelligence, and machine learning, are basically changing spectral management into something more predictive, and also adaptive process that keeps adjusting itself. With AI supported cultivation systems, we get a mix of environmental sensors plus imaging tech, some physiological readings too, and then predictive rules or algorithms running in the background. These tools then tune the spectral composition based on the crop actual status, developmental stage, and all those day-to-day environmental swings (2,12). In practice this tends to boost cultivation precision, while also cutting down on energy waste that comes from static lighting routines. And there's more, sensor guided automation lets irrigation, nutrient delivery and climate control be optimized in sync together with the spectrum management, instead of treating them like separate issues.

Recent engineering studies keep showing that putting AI into spectral spatial optimization models can help with photon dispersal and also better environmental steadiness in plant factory systems. (45) said spectral spatial optimization improved canopy-level photon distribution and it also cut down on wasted or unnecessary energy use, especially during multilayer cultivation conditions. In a similar direction, (44) came up with lighting strategies built around a Gaussian distribution for microgreen cultivation, and those choices enhanced biomass uniformity as well as light use efficiency. Altogether these results point to plant physiology working together with computational modelling and engineering optimization, which is more like a next generation way of building CEA systems.

More dynamic lighting work also adds that omics assisted optimization might help plants adjust to long photoperiods and continuous light settings. (21) demonstrated that alternating spectral regimes affected cyclic electron transport, photosystem steadiness, circadian alignment, and how biomass gets portioned under continuous light cultivation. So, it seems like upcoming spectral optimization plans will rely more on pulling together molecular data, physiological measurements, and engineering datasets, rather than using only a simple wavelength-based approach.

Despite pretty major progress, some limitations still persist. Spectral responses can be very genotype dependent and the inconsistencies in photoperiod handling, shifting environmental conditions, and the way experiments are designed, makes it harder to craft generalized, forward-looking predictive models. On top of that, omics analyses spit out huge multidimensional datasets that basically need serious computational infrastructure, plus standardized analytical workflows. Also, a lot of AI based cultivation systems are still kind of hard to generalize beyond tightly controlled experimental setups.

Bringing together omics tools, high throughput phenotyping, and AI supported environmental control is turning spectral engineering into more of a predictive, metabolically guided field. With ongoing improvements in computational biology, adaptive lighting technologies, and smarter regulation of the cultivation climate, the next step should speed up the creation of cultivation platforms that are highly optimized. The goal is to boost productivity and also enhance phytochemical value, stress resilience, and energy efficiency, all at once, especially in controlled environment agriculture.

Crop-Specific Applications of Spectral Engineering in Controlled Environment Agriculture

The pronounced variability of light-induced physiological responses across species, cultivars, and developmental phases underscores a fundamental challenge in controlled-environment agriculture (CEA); maximizing the efficacy of spectral engineering dictates crop-specific optimization over generic, multi-purpose lighting configurations. A bunch of recent work across leafy vegetables, herbs, microgreens and fruit crops shows that programmable spectral environments can steer morphology, physiology, phytochemical buildup, yield, and even postharvest quality but it all depends on the particular crop's metabolic wiring, not just "more light" or "better light" in general.

Leafy vegetables are honestly among the most heavily studied targets in spectral engineering, partly because they cycle fast, and they react strongly to light quality. In lettuce, (22) showed that spectral composition changed biomass build up, chlorophyll levels, and overall physiological performance, and also that cultivars differ enough to change how big the response is. In a similar way (24) described how red–blue spectral mixes could raise photosynthetic efficiency and vegetative growth compared with monochromatic setups, yet when red light ran too dominant it pushed elongated growth forms and made plants less compact. Overall, these results underline that growers have to strike a balance between quick biomass production and marketable appearance.

Spectral control also shifts nutrient make up and phytochemical accumulation in lettuce systems. (43) reported that planned pre-harvest illumination programs lowered nitrate levels while raising total phenolic content and antioxidant activity in hydroponic green oak lettuce. That's commercially relevant because it boosts nutritional quality, without really messing up productivity or stretching cultivation time too much. The influence of spectral quality on secondary metabolite accumulation and nutraceutical traits in horticultural crops is summarized in **Table 3**.

Table 3. Crop-Specific Responses to Spectral Engineering in Horticultural Crops

Crop	Spectral Treatment	Major Response	Key Outcome	Reference
Lettuce	Red + blue LEDs	Enhanced photosynthesis and phenolic accumulation	Improved biomass and nutritional quality	(22,30,43)
Basil	Blue/red LEDs	Altered volatile organic compounds and pigmentation	Improved flavour and aroma quality	(11,42)
Celery	Blue-light supplementation	Enhanced antioxidant activity and flavonoid biosynthesis	Improved physiological quality	(17,30)
Strawberry	Blue + UV treatments	Increased anthocyanin biosynthesis	Improved coloration and antioxidant activity	(11)
Brassica microgreens	Mixed LED spectra	Metabolomic reprogramming and phytochemical enrichment	Enhanced nutraceutical quality	(8,23,44)

Celery shows pretty clear physiological and metabolic reactions when blue-light is added, and also when light intensity is handled, in a more managed way. (26) found that supplementing with blue light can boost chlorophyll build-up, raise antioxidant enzyme performance, and improve photosynthetic efficiency, yet at the same time it changes leaf shape and the source–sink relationship. In another related work (39) said light intensity controlled how flavonoids accumulate, how carotenoids are synthesized, and how antioxidant metabolism proceeds, mainly by shifting phenylpropanoid- connected enzyme activity and transcription-based routes. Taken together these results imply that celery quality responds strongly to the combined adjustment of spectral composition along with the irradiance level.

Herbs plus specialty crops also seem to be very sensitive to spectra in a way that ties to aroma, taste, and appearance quality. For basil (42) reported that narrowband blue and red LED settings changed the volatile organic compound patterns, which connect back to flavour notes and even consumer acceptability. Then (27) went further and demonstrated that tweaking the spectrum influenced basil structure, chlorophyll fluorescence, pigmentation, and what happens after harvest in terms of quality traits. All of this basically highlights that physiological readouts and sensory or culinary quality evaluations should be considered together for culinary herbs.

Microgreens and Brassica vegetables, have turned into big targets for spectral engineering mainly because they pack a high phytochemical density and they grow in such short cycles. (37) showed that LED spectral conditions can shift metabolomic profiles quite a lot, plus, the antioxidant-linked metabolites in Brassica microgreens. In other words, these reactions suggest that the spectral surroundings, can be tuned to boost nutraceutical value and improve functional food quality, even within young plant tissues.

Spectral responses in fruit crops are inherently more complex and stage-dependent, driven by the dynamic intersection of ripening mechanisms, pigment accumulation, and reciprocal hormonal regulation. For example, in strawberry, (11) reported that light quality had a strong effect on anthocyanin biosynthesis, on coloration, and on several fruit quality traits, by steering structural genes and also transcriptional genes tied to flavonoid metabolism. UV related treatments also seemed to increase epidermal pigmentation and antioxidant buildup via stress signalling pathways, but the outcomes were not uniform different cultivars responded differently, and developmental stages also needed attention.

These studies together, show that spectral optimization has to be tuned based on crop physiology, where the plants are in their development, what the producer actually wants, and what the market expects. Lighting setups that were tuned mainly for biomass output might not also push phytochemical accumulation or make the taste and sensory quality better, and vice versa. Also, if we choose treatments that strongly boost secondary metabolism, we might unintentionally shrink vegetative growth, or waste energy efficiency, in practical terms. So going forward, crop specific spectral engineering will likely rely on a more blended optimization, linking plant physiology, metabolic responses, environmental management, and long term economic sustainability inside today's CEA systems.

Challenges, Limitations, and Future Perspectives of Spectral Engineering in Controlled Environment Agriculture

Despite major advances in programmable lighting systems and environmental control technologies, quite a few scientific, technical, and economic limitations keep showing up and they still restrict large-scale use of spectral engineering in controlled environment agriculture (CEA). A primary challenge system from the fact that plant responses to distinct spectral environments are highly contingent upon species, cultivar, and developmental stage, precluding the application of simplified or universal regulatory principles. Basically, the exact same spectral treatment can lead to pretty different physiological and metabolic outcomes across crops, because of shifts in photoreceptor sensitivity, canopy architecture, nutrient demand, and also the way stress acclimation capacity is handled. Because of that, universal spectral recipes are rarely usable across diverse horticultural production systems (1).

Another major limitation is the complicated, interaction between light and other surroundings variables, like temperature, humidity, CO_2 concentration, nutrient availability, airflow, and photoperiod. Many studies end up evaluating spectral effects under very controlled experimental setups that may not really match what happens in commercial cultivation. (3) pointed out that environmental interactions really do steer crop physiology, postharvest quality, and resource use efficiency, so it makes sense to push integrated environmental management instead of treating spectral optimization as a stand alone fix. On top of that there are also inconsistencies in spectral protocols, photon flux density, light duration, and the way reporting is done, which often muddles cross study comparisons and really lowers reproducibility.

Energy consumption still stays one of the biggest and critical barriers, holding back the commercial expansion of plant factory systems using artificial lighting (PFALs). In fact, artificial lighting plus the HVAC systems together makes up the largest share of energy demand inside indoor farming sites. (12) said that lighting and HVAC systems basically dominate PFAL energy use, and they also mentioned that tuning light intensity, adjusting spectral distribution, planning photoperiod schedules, and managing HVAC operation properly could noticeably lower energy use and carbon emissions. That same review went further, pointing to renewable-energy integration as well, plus artificial intelligence assisted control systems, and even improved energy materials, all of which can help indoor agriculture stay more sustainable over the long run.

Economic feasibility is pretty tightly connected to energy use efficiency and the whole infrastructure cost. (50) showed that putting photovoltaics into the setup together with architectural energy saving methods can really cut down primary energy consumption and greenhouse gas emissions in plant factories, even if the installation expenses still stay high. Their economic review also suggests that investment payback timelines for PFAL systems might keep being commercially reasonable when energy saving technologies and renewable-energy components are blended in the right way. Still, the big capital outlay, ongoing operating costs, and the technological complexity keep acting like brakes on wide adoption, especially in areas that are resource constrained.

Dynamic lighting systems and continuous-light cultivation approaches also bring physiological limitations. If the photoperiod is kept long, it can trigger chlorosis, oxidative imbalance, carbohydrate accumulation type disorders and even photosystem instability, unless spectral timing is handled well and circadian regulation is tuned properly. (21) found that acclimation to continuous-light environments leans heavily on spectral scheduling, and on regulating cyclic electron transport and the stability of the photosystem. So the takeaway is that next generation lighting systems have to weave photobiology with circadian control, plus stress physiology, so productivity losses don't show up during prolonged illumination.

Even though omics technology, artificial intelligence, and digital agriculture platforms are quickly reshaping spectral engineering research, there are still a few limitations, when it comes to actually using them in the field. AI helped cultivation systems usually need huge datasets, strong computational power, and pretty standardized environmental measurements, otherwise the forecasting and automation don't stay reliable. (51) also mentioned that deep-learning work in CEA right now is still strained by microclimate variability, small or limited training datasets, weak model transferability, and questions around economic sustainability. In a similar way, digital twin approaches are still in somewhat early adoption for agriculture, even if they promise predictive cultivation, simulation driven optimization, and automatic environmental regulation.

More recent reviews on digital twins underline that interoperability, real time synchronization, data standardization, and bringing together diverse sensor networks are still big technical hurdles in smart agriculture systems (52,53). On top of that, getting IoT sensors at scale, hyperspectral imaging, machine learning pipelines, and adaptive environmental control to work together consistently demands a solid cyber physical backbone and computational frameworks that are not yet available everywhere.

Future developments in spectral engineering are likely to drift toward adaptive and crop specific environmental management schemes, tying together real time phenotyping, omics enabled metabolic modelling, digital twin frameworks, and AI based predictive control. With progress in deep learning, sensor networks, edge computing, and computational biology, it should get easier to tune the spectral environment on the fly, depending on crop developmental stage, the metabolic condition, and those shifting environmental swings. Also, integrating renewable energy setups, energy efficient lighting architectures, and smart climate control tooling will be important, not just for sustainability but for commercial scale up of PFAL systems. Emerging applications of spectral engineering integrated with omics technologies, artificial intelligence, and smart cultivation systems are summarized in **Table 4**.

Table 4. Major Challenges and Future Directions in Spectral Engineering

Major Challenge	Current Limitation	Future Direction	Reference

Energy consumption	High electricity demand in PFAL systems	Renewable-energy integration and smart energy management	(12)
Spectral standardization	Inconsistent experimental protocols	Development of universal reporting frameworks	(45)
AI scalability	Limited datasets and model transferability	Robust predictive and adaptive AI systems	(13)
Digital twin implementation	Interoperability and infrastructure limitations	Integrated cyber-physical cultivation platforms	(52,53)
Economic feasibility	High infrastructure and operational costs	Cost-efficient smart cultivation technologies	(50)

For future work, researchers should give more attention to long term cultivation output, lifecycle assessment, economic viability, and environmental sustainability, instead of staying only on short term physiological signals. Better harmonization of spectral protocols, improved reproducibility of experimental conditions, and deeper bridging between plant science, engineering, computational biology, and environmental economics will be needed to push next generation-controlled environment agriculture ahead. Overall, even with major technical and economic hurdles, spectral engineering remains as one of the most promising routes for precision regulation of plant metabolism, sustainable food production, and more intelligent indoor agriculture.

CONCLUSION AND FUTURE OUTLOOK

Spectral engineering has become a big strategy for precise regulation of plant growth, metabolism, and nutritional quality within controlled environment agriculture (CEA). Lately, advances in programmable LED systems allow more or less targeted engineering of spectral composition, light intensity, photoperiod, and even the timing of illumination, all aligned with crop specific physiological and developmental needs. In many different horticultural setups, well designed spectral environments help steer photosynthesis, carbon assimilation, nitrogen metabolism, antioxidant performance, secondary metabolite production, plant form, yield, and also postharvest quality (8,35,39).

Plant responses to spectral conditions are not static, they are rather dynamic and they swing a lot depending on species, genotype, developmental phase, and what else is happening in the environment. Blue, red, green, far-red, and ultraviolet wavelengths each bring their own regulatory contributions, mostly via photoreceptor signalling, circadian pathways, ROS steadiness, and downstream metabolic routes. But importantly, spectral engineering doesn't really work from single wavelengths alone. It needs a combined, and crop tailored spectral game plan that can balance productivity, phytochemical enrichment, stress acclimation, and resource-use efficiency.

Recent integration of metabolomics, transcriptomics, high throughput phenotyping and artificial intelligence has expanded the scope of spectral engineering research. Machine learning, IoT assisted sensing systems and digital twin technologies are increasingly making possible predictive cultivation, and adaptive environmental control in plant factory systems (51,53). Also, advances in dynamic lighting setups and spectral spatial optimization have helped clarify, how temporal and spatial light distributions affect canopy level photosynthetic efficiency and the metabolic regulation in practice (44,45).

Even so, despite that progress, there are still important scientific and commercial limitations that really matter. Spectral responses can vary strongly among different crops, and cultivation systems, while inconsistencies in experimental protocols keep interfering with reproducibility and large scale standardization. On top of that, the high energy demand tied to lighting and HVAC systems remains a major headache in PFAL based agriculture. Recent work keeps highlighting that combining renewable energy, energy efficient lighting designs, and smart environmental control will be essential for better economic feasibility as well as environmental sustainability in indoor farming setups (12,50).

Future research should more and more look into crop specific and growth stage specific spectral tuning, supported by systems biology, computational modeling, and real-time phenotyping, rather than doing the same thing for everything. It will be necessary to build tighter links between photobiology, artificial intelligence, digital agriculture, engineering, and environmental economics, so adaptive growing setups can be made that improve productivity, nutritional quality, stress resistance and energy-use efficiency at the same time. Also, long term checking of lifecycle sustainability, economic scale-up feasibility, and commercialization potential should become a main priority for future controlled environment agriculture work. Not only in short trials but across real ground conditions.

Overall, spectral engineering is a quickly changing multidisciplinary area with big consequences for sustainable food production, urban agriculture, and cultivation systems that can handle climate stress. Continued progress in smart environmental regulation, omics assisted crop optimization, and energy saving cultivation technologies should help speed up next-generation indoor farming systems, designed to respond to future global food security issues.

REFERENCE:

1. Cowan N, Ferrier L, Spears B, Drewer J, Reay D, Skiba U. CEA Systems: the Means to Achieve Future Food Security and Environmental Sustainability? Front Sustain Food Syst. 2022 Jun 15;6:891256. doi:10.3389/fsufs.2022.891256
2. Srimal MDW, Aboobucker MSM, Sha HH, Anjum R, Ahmed MR, Raja Rani T. Emerging Frontiers in CEA: An IoT-Based System Architecture for Smart, Sustainable, and High-Yielding Controlled Environment Agriculture. IOP Conf Ser Earth Environ Sci. 2024 Oct 1;1401(1):012004. doi:10.1088/1755-1315/1401/1/012004
3. Gruda NS, Li X, Gallegos-Cedillo VM, Samouline G, Dong J, Weiss J, et al. From growth to table: exploring the impact of pre-harvest conditions on greenhouse vegetable quality. Eur J Hortic Sci. 2025 Sep 3;ejhs.2025.0019. doi:10.1079/ejhs.2025.0019
4. Yilmaz H, Yilmaz A. Hidden Hunger in the Age of Abundance: The Nutritional Pitfalls of Modern Staple Crops. Food Sci Nutr. 2025 Feb;13(2):e4610. doi:10.1002/fsn3.4610
5. Fraser DP, Hayes S, Franklin KA. Photoreceptor crosstalk in shade avoidance. Curr Opin Plant Biol. 2016 Oct;33:1–7. doi:10.1016/j.pbi.2016.03.008
6. Kong Y, Zheng Y. Multiple Signals Can Be Integrated into Pathways of Blue-Light-Mediated Floral Transition: Possible Explanations on Diverse Flowering Responses to Blue Light Manipulation. Agronomy. 2025 Jun 25;15(7):1534. doi:10.3390/agronomy15071534
7. Kusuma P, Pattison PM, Bugbee B. From physics to fixtures to food: current and potential LED efficacy. Hortic Res. 2020 Dec;7(1):56. doi:10.1038/s41438-020-0283-7
8. Paradiso R, Proietti S. Light-Quality Manipulation to Control Plant Growth and Photomorphogenesis in Greenhouse Horticulture: The State of the Art and the Opportunities of Modern LED Systems. J Plant Growth Regul. 2022 Feb;41(2):742–80. doi:10.1007/s00344-021-10337-y
9. Ma Y, Ma X, Gao X, Wu W, Zhou B. Light Induced Regulation Pathway of Anthocyanin Biosynthesis in Plants. Int J Mol Sci. 2021 Oct 15;22(20):11116. doi:10.3390/ijms222011116
10. Trivellini A, Toscano S, Romano D, Ferrante A. The Role of Blue and Red Light in the Orchestration of Secondary Metabolites, Nutrient Transport and Plant Quality. Plants. 2023 May 18;12(10):2026. doi:10.3390/plants12102026
11. Wang F, Wang J, Ji G, Kang X, Li Y, Hu J, et al. Regulation of Anthocyanins and Quality in Strawberries Based on Light Quality. Horticulturae. 2025 Mar 31;11(4):377. doi:10.3390/horticulturae11040377
12. Cai W, Bu K, Zha L, Zhang J, Lai D, Bao H. Energy consumption of plant factory with artificial light: Challenges and opportunities. Renew Sustain Energy Rev. 2025 Mar;210:115235. doi:10.1016/j.rser.2024.115235
13. Cembrowska-Lech D, Krzemińska A, Miller T, Nowakowska A, Adamski C, Radaczyńska M, et al. An Integrated Multi-Omics and Artificial Intelligence Framework for Advance Plant Phenotyping in Horticulture. Biology. 2023 Sep 30;12(10):1298. doi:10.3390/biology12101298
14. D'Amico-Damião V, Carvalho RF. Cryptochrome-Related Abiotic Stress Responses in Plants. Front Plant Sci. 2018 Dec 19;9:1897. doi:10.3389/fpls.2018.01897
15. Pierik R, Ballaré CL. Control of Plant Growth and Defense by Photoreceptors: From Mechanisms to Opportunities in Agriculture. Mol Plant. 2021 Jan;14(1):61–76. doi:10.1016/j.molp.2020.11.021
16. Liu H, Lin R, Deng XW. Photobiology: Light signal transduction and photomorphogenesis. J Integr Plant Biol. 2020 Sep;62(9):1267–9. doi:10.1111/jipb.13004
17. Chibani K, Gherli H, Fan M. The role of blue light in plant stress responses: modulation through photoreceptors and antioxidant mechanisms. Front Plant Sci. 2025 May 16;16:1554281. doi:10.3389/fpls.2025.1554281
18. Wei Y, Wang S, Yu D. The Role of Light Quality in Regulating Early Seedling Development. Plants. 2023 Jul 24;12(14):2746. doi:10.3390/plants12142746
19. Mujahid M, Ambreen A, Zarlashat Y, Sarfraz Z, Iqbal MS, Waheed A, et al. Integration of Light and Circadian Signaling in Plant Gene Regulatory Networks: Implications for Photomorphogenesis and Stress Adaptation. Biology. 2025 Oct 8;14(10):1375. doi:10.3390/biology14101375
20. Liebers M, Pfannschmidt T. New horizons in light control of plant photomorphogenesis and development. Front Photobiol. 2024 Jan 8;1:1346705. doi:10.3389/fphbi.2023.1346705
21. Marie TRJG, Leonardos ED, Rana N, Grodzinski B. Tomato and mini-cucumber tolerance to photoperiodic injury involves photorespiration and the engagement of nighttime cyclic electron flow from dynamic LEDs. Front Plant Sci. 2024 May 22;15:1384518. doi:10.3389/fpls.2024.1384518
22. Alrajhi AA, Alsahli AS, Alhelal IM, Rihan HZ, Fuller MP, Alsadon AA, et al. The Effect of LED Light Spectra on the Growth, Yield and Nutritional Value of Red and Green Lettuce (Lactuca sativa). Plants. 2023 Jan 19;12(3):463. doi:10.3390/plants12030463
23. Tang Y, Mao R, Guo S. Effects of LED spectra on growth, gas exchange, antioxidant activity and nutritional quality of vegetable species. Life Sci Space Res. 2020 Aug;26:77–84. doi:10.1016/j.lssr.2020.05.002

24. Soufi HR, Roosta HR, Fatehi F, Ghorbanpour M. Spectral composition of LED light differentially affects biomass, photosynthesis, nutrient profile, and foliar nitrate accumulation of lettuce grown under various replacement methods of nutrient solution. Food Sci Nutr. 2023 Dec;11(12):8143–62. doi:10.1002/fsn3.3735
25. Zhu Y, Patil BS, Zhen S. From ultraviolet-B to red photons: Effects of end-of-production supplemental light on anthocyanins, phenolics, ascorbic acid, and biomass production in red leaf lettuce. Anand Gururani, M, editor. PLOS One. 2025 Jul 30;20(7):e0328303. doi:10.1371/journal.pone.0328303
26. Dou H, Li Z, Liu Q, Jiang P, Song J, Ji F, et al. Organ-Specific Physiological and Metabolic Differentiation in Celery (Apium graveolens L.) to Supplemental Blue Light in Controlled Environment Agriculture. Horticulturae. 2025 Sep 5;11(9):1074. doi:10.3390/horticulturae11091074
27. Oehler MA, Kelly N, Fonseca JM, Evensen E, Park E, Gu G, et al. Influence of Supplementary Blue and Far-Red Light on the Morphology and Texture of Ocimum basilicum L. Grown in Controlled Environments. Horticulturae. 2025 Mar 6;11(3):287. doi:10.3390/horticulturae11030287
28. Liu J, Van Iersel MW. Photosynthetic Physiology of Blue, Green, and Red Light: Light Intensity Effects and Underlying Mechanisms. Front Plant Sci. 2021 Mar 5;12:619987. doi:10.3389/fpls.2021.619987
29. Smith HL, McAusland L, Murchie EH. Don't ignore the green light: exploring diverse roles in plant processes. J Exp Bot. 2017 Apr 1;68(9):2099–110. doi:10.1093/jxb/erx098
30. Van Brenk JB, Courbier S, Kleijweg CL, Verdonk JC, Marcelis LFM. Paradise by the far-red light: Far-red and red:blue ratios independently affect yield, pigments, and carbohydrate production in lettuce, Lactuca sativa. Front Plant Sci. 2024 Apr 30;15:1383100. doi:10.3389/fpls.2024.1383100
31. Al Murad M, Razi K, Jeong BR, Samy PMA, Muneer S. Light Emitting Diodes (LEDs) as Agricultural Lighting: Impact and Its Potential on Improving Physiology, Flowering, and Secondary Metabolites of Crops. Sustainability. 2021 Feb 12;13(4):1985. doi:10.3390/su13041985
32. Li L, Sugita R, Yamaguchi K, Togawa H, Terashima I, Yamori W. High-precision lighting for plants: monochromatic red laser diodes outperform LEDs in photosynthesis and plant growth. Front Plant Sci. 2025 May 20;16:1589279. doi:10.3389/fpls.2025.1589279
33. Häder DP. Photosynthesis in Plants and Algae. Anticancer Res. 2022 Oct;42(10):5035–41. doi:10.21873/anticanres.16012
34. Wu W, Chen L, Liang R, Huang S, Li X, Huang B, et al. The role of light in regulating plant growth, development and sugar metabolism: a review. Front Plant Sci. 2025 Jan 7;15:1507628. doi:10.3389/fpls.2024.1507628
35. Ramezani M, Thompson D, Moreno M, Joshi V. Biochemical repercussions of light spectra on nitrogen metabolism in spinach (Spinacia oleracea) under a controlled environment. Front Plant Sci. 2023 Dec 20;14:1283730. doi:10.3389/fpls.2023.1283730
36. Profico CM, Nicola S. Selenium biofortification and LED management in controlled-environment agriculture: advances, synergies and future perspectives. Eur J Hortic Sci. 2026 Apr 14;ejhs.2026.0006. doi:10.1079/ejhs.2026.0006
37. Li Y, Zhou B, Teng Z, Zhang M, Yu L, Luo Y, et al. Improved metabolomic approach for evaluation of phytochemicals in mustard, kale, and broccoli microgreens under different controlled environment agriculture conditions. J Agric Food Res. 2023 Dec;14:100719. doi:10.1016/j.jafr.2023.100719
38. Gawande V, Priya, Raut D, Rai S, Beese S, Singh BV, et al. Artificial Light Spectra and Its Impact on Plant Physiological Processes and Secondary Metabolism. Int J Plant Soil Sci. 2023 Aug 11;35(18):2060–70. doi:10.9734/ijpss/2023/v35i183492
39. Qin Y, Liu X, Li C, Chu Q, Cheng S, Su L, et al. Effect of light intensity on celery growth and flavonoid synthesis. Front Plant Sci. 2024 Jan 16;14:1326218. doi:10.3389/fpls.2023.1326218
40. Kim CK, Eom SH. Light Controls in the Regulation of Carotenoid Biosynthesis in Leafy Vegetables: A Review. Horticulturae. 2025 Feb 1;11(2):152. doi:10.3390/horticulturae11020152
41. Wang G, Sun X, Li Y, Wang Y, Jin C. The role of UV-B radiation in modulating secondary metabolite biosynthesis and regulatory mechanisms in medicinal plants. Bio Resources. 2025 Feb 5;20(2). doi:10.15376/biores.20.2.Wang
42. Hammock HA, Kopsell DA, Sams CE. Narrowband Blue and Red LED Supplements Impact Key Flavor Volatiles in Hydroponically Grown Basil Across Growing Seasons. Front Plant Sci. 2021 Feb 26;12:623314. doi:10.3389/fpls.2021.623314
43. Htwe. Pre-harvest illumination with different spectral compositions improves quality of green oak lettuce in hydroponic system. Agric Nat Resour. 2023;57(5). doi:10.34044/j.anres.2023.57.5.11
44. Silva MD, Vasconcelos JM, Silva FBD, Bailão ASDO, Guedes ÍMR, Vilela MDS, et al. Growing in red: impact of different light spectra and lighting conditions on lentil microgreens growth in vertical farming. Front Plant Sci. 2024 Dec 23;15:1515457. doi:10.3389/fpls.2024.1515457
45. Wang Z, Huang H, Shi M, Xiong Y, Wang J, Wang Y, et al. Optimized Spectral and Spatial Design of High-Uniformity and Energy-Efficient LED Lighting for Italian Lettuce Cultivation in Miniature Plant Factories. Horticulturae. 2025 Jul 3;11(7):779. doi:10.3390/horticulturae11070779
46. Parrish CH, Hebert D, Jackson A, Ramasamy K, McDaniel H, Giacomelli GA, et al. Optimizing spectral quality with quantum dots to enhance crop yield in controlled environments. Commun Biol. 2021 Jan 27;4(1):124. doi:10.1038/s42003-020-01646-1

47. Beatrice P, Chiatante D, Scippa GS, Montagnoli A. Photoreceptors' gene expression of Arabidopsis thaliana grown with biophilic LED-sourced lighting systems. Foulkes NS, editor. PLOS ONE. 2022 Jun 10;17(6):e0269868. doi:10.1371/journal.pone.0269868
48. Wang P, Zhang H, Yin Y, Ge Y, Chen B, Hu J, et al. Differential epigenetic regulation by blue and UV-A light reveals the key role of CsSDG36-mediated H3K4 methylation in leaf development and secondary metabolism in Camellia sinensis. Genome Biol. 2025 Jun 2;26(1):150. doi:10.1186/s13059-025-03618-2
49. Ashenafi EL, Nyman MC, Holley JM, Mattson NS. The influence of LEDs with different blue peak emission wavelengths on the biomass, morphology, and nutrient content of kale cultivars. Sci Hortic. 2023 Jul;317:111992. doi:10.1016/j.scienta.2023.111992
50. Kim Y, Shin HR, Oh S hyun, Yu KH. Analysis on the Economic Feasibility of a Plant Factory Combined with Architectural Technology for Energy Performance Improvement. Agriculture. 2022 May 11;12(5):684. doi:10.3390/agriculture12050684
51. Ojo MO, Zahid A. Deep Learning in Controlled Environment Agriculture: A Review of Recent Advancements, Challenges and Prospects. Sensors. 2022 Oct 19;22(20):7965. doi:10.3390/s22207965
52. Subeesh A, Chauhan N. Agricultural digital twin for smart farming: A review. Green Techno Sustain. 2026 Apr;4(2):100299. doi:10.1016/j.grets.2025.100299
53. Zhang R, Zhu H, Chang Q, Mao Q. A Comprehensive Review of Digital Twins Technology in Agriculture. Agriculture. 2025 Apr 22;15(9):903. doi:10.3390/agriculture15090903
54. Wei J, Ni L, Luo L, Chen M, You M, Sun Y, et al. GFS-YOLO11: A Maturity Detection Model for Multi-Variety Tomato. Agronomy. 2024 Nov 9;14(11):2644. doi:10.3390/agronomy14112644