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Light as Energy and Information in Plant Growth, Development and Flowering: An Integrative Critical Review

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Authors' contributions

This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

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Review Article

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Abstract

Light occupies a singular position in plant biology because it supplies the energy for photosynthetic carbon gain while simultaneously providing information about time, season, canopy proximity, spatial orientation and environmental change. These energetic and informational functions are sensed across different scales and are integrated with endogenous developmental programmes, the circadian system, hormone signalling and temperature responses. This critical narrative review evaluates how light quantity, spectral quality, photoperiod, direction and temporal dynamics regulate plant growth, development and flowering, with particular emphasis on higher plants and on the translation of mechanistic knowledge from *Arabidopsis thaliana* to crops and controlled-environment horticulture. Literature was selected through live searches of accessible scholarly databases and indexes, with emphasis on peer-reviewed primary research, authoritative reviews and verifiable bibliographic records. The evidence is strongest for a conserved core in which phytochromes, cryptochromes, phototropins and UV RESISTANCE LOCUS 8 feed into interconnected regulators such as PHYTOCHROME-INTERACTING FACTOR proteins, CONSTITUTIVELY PHOTOMORPHOGENIC 1 and ELONGATED HYPOCOTYL 5. These networks coordinate de-etiolation, shade responses, organ growth and temporal development. Flowering provides the clearest example of light-time integration: circadian gating and photoreceptor control converge on florigenic signals, yet the upstream wiring differs substantially among long-day and short-day crops. Evidence from photosynthetic physiology also challenges simple wavelength rankings. Green and far-red photons can contribute substantially under high irradiance or within canopies, while spectral effects on growth often depend on photon dose, developmental stage and canopy architecture. Controlled-environment studies demonstrate practical opportunities for spectral

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and temporal manipulation, but generalisation is limited by cultivar specificity, short experimental duration, inconsistent spectral reporting and confounding between spectrum, daily light integral and temperature. Future work should integrate photoreceptor genetics, whole-canopy carbon balance, dynamic lighting and reproductive phenology under realistic fluctuating environments. Light is therefore best treated not as a single growth factor but as a multidimensional environmental signal whose effects emerge from context-dependent integration across molecular, organ and whole-plant scales.

Keywords: Photomorphogenesis; phytochrome; cryptochrome; daily light integral; shade avoidance; circadian clock; florigen; controlled-environment agriculture.

1. Introduction

Light is an environmental resource and a developmental signal, and these two functions are inseparable in intact plants. Solar photons drive the light reactions of photosynthesis, thereby constraining the carbon and energy available for growth, yet the same radiation field also conveys information about whether a seedling has emerged into daylight, whether neighbouring leaves are approaching, which direction offers open space, what time of day it is and whether seasonal day length is compatible with reproduction. Plants therefore do not respond to "light" as a unitary variable. They interpret photon quantity, spectral composition, duration, direction and fluctuation through partially overlapping photosynthetic, photoreceptor and circadian systems (Chen *et al.*, 2004; Paik & Huq, 2019; Poorter *et al.*, 2019).

This multidimensionality explains why apparently simple questions, such as whether blue or red light is "better" for growth, often produce contradictory answers. Spectral treatments can alter photosynthetic efficiency, leaf anatomy, stomatal behaviour, chloroplast positioning, internode elongation and resource allocation at the same time. If total photon flux, daily light integral (DLI), leaf temperature, background spectrum or developmental stage differs among treatments, observed changes cannot be attributed confidently to wavelength alone. At canopy scale, the problem becomes more complex because photons that are weakly absorbed in upper leaves may penetrate to lower leaves and contribute disproportionately to whole-canopy carbon gain. The classical action spectrum of leaf photosynthesis remains foundational, but subsequent work has shown that its interpretation depends on irradiance, absorptance and optical depth within leaves and canopies (McCree, 1971; Terashima *et al.*, 2009; Zhen & Bugbee, 2020).

In parallel with photosynthetic physiology, molecular genetics has established a sophisticated light-sensing architecture. Red and far-red radiation are perceived principally through phytochromes; blue and ultraviolet-A radiation through cryptochromes and phototropins; and ultraviolet-B through UV RESISTANCE LOCUS 8 (UVR8). These receptors converge on regulatory hubs that include PHYTOCHROME-INTERACTING FACTORs (PIFs), CONSTITUTIVELY PHOTOMORPHOGENIC 1 (COP1), SUPPRESSOR OF PHYA proteins and ELONGATED HYPOCOTYL 5 (HY5), linking perception to large-scale transcriptional and proteostatic changes (Cheng *et al.*, 2021; Christie, 2007; Jenkins, 2014; Leivar & Monte, 2014). The result is not a collection of independent colour-specific pathways but a network whose output depends on receptor co-action, developmental history and the physiological state of the plant. A recent synthesis of plant light signalling further emphasises that phytochrome and cryptochrome pathways operate through interacting nuclear regulatory processes rather than as isolated wavelength-specific responses (Huq *et al.*, 2024).

The consequences extend throughout development. Light governs the transition from skotomorphogenesis to photomorphogenesis after emergence, influences leaf expansion and chloroplast development, modulates root-shoot allocation, regulates phototropism and shade avoidance, entrains circadian rhythms and provides seasonal information for reproductive transition. Light signalling also intersects extensively with auxin and gibberellin pathways, allowing environmental information to reshape cell elongation and organ architecture (de Lucas *et al.*, 2008; Feng *et al.*, 2008; Tao *et al.*, 2008). This integration is especially important in dense vegetation, where a low red-to-far-red ratio can trigger elongation before severe photosynthetic shade develops, and in warming environments, because phytochrome B also participates in temperature sensing (Jung *et al.*, 2016; Legris *et al.*, 2016).

Flowering is the most intensively resolved example of light-dependent developmental timing. In *Arabidopsis thaliana*, photoperiodic flowering depends on coincidence between circadian phase and external light, stabilisation and activity of CONSTANS (CO), and induction of FLOWERING LOCUS T (FT), whose product participates in long-distance floral signalling (Corbesier *et al.*, 2007; Song *et al.*, 2015; Turck *et al.*, 2008). Yet this apparently canonical scheme cannot be transferred unchanged to crops. Rice, barley and wheat contain homologous or analogous components whose regulatory signs and network positions have diverged during evolution and domestication, creating short-day, long-day and photoperiod-insensitive phenotypes (Beales *et al.*, 2007; Hayama *et al.*, 2003; Turner *et al.*, 2005). Consequently, a mechanistically correct account of light-regulated flowering must distinguish conserved output logic from lineage-specific upstream control. Recent syntheses of crop photoperiodism similarly indicate that circadian-clock and photoperiod pathways retain shared components while their regulatory deployment varies among crop species and domestication histories (Yang *et al.*, 2024; González-Delgado *et al.*, 2025).

Several recent reviews have addressed photoreceptor networks, photoperiodism, greenhouse spectral manipulation, light stress or light-regulated metabolism, but these domains are commonly treated in isolation (Gendron & Staiger, 2023; Paik & Huq, 2019; Paradiso & Proietti, 2022; Wu *et al.*, 2025). A synthesis that connects photon capture, photoreceptor signalling, circadian timing, flowering and controlled-environment translation is needed because experimental conclusions at one level can be misleading when extrapolated to another. The central problem is therefore not simply to catalogue effects of wavelengths or day lengths, but to assess which light responses are mechanistically established, which depend strongly on context and where the evidence is too methodologically heterogeneous for general prescriptions. Recent controlled-environment evidence also reinforces that plant

responses to artificial lighting depend jointly on spectrum, intensity and photoperiod, limiting the transferability of fixed light recipes across crops and cultivars (Azizi *et al.*, 2025).

1.1 Scope, Research Gap and Objectives

This review focuses on higher plants, using *Arabidopsis thaliana* as the principal mechanistic model while incorporating crop and horticultural evidence where it tests generality or demonstrates translational value. It considers light quantity, spectral quality, photoperiod, direction and temporal dynamics as interacting determinants of vegetative growth, developmental plasticity, circadian organisation and floral transition. Photosynthetic biochemistry is discussed when it affects development or interpretation of whole-plant growth responses, rather than as a comprehensive treatment of photosynthesis. Algal and cyanobacterial photobiology, detailed ultraviolet toxicology and engineering aspects of lighting hardware are outside the central scope. The principal gap addressed is the persistent separation between molecular photomorphogenesis, photosynthetic light-use physiology, photoperiodic flowering and controlled-environment practice. The objectives are to integrate these literatures, evaluate the strength and transferability of their evidence, identify sources of experimental disagreement and define research priorities that can connect receptor-level mechanisms with crop performance and reproductive timing.

2. Methods for Literature Selection

2.1 Review Design and Rationale

A critical narrative review design was selected because the topic spans molecular genetics, photophysics, ecophysiology, crop phenology and horticultural production, with outcomes that are too heterogeneous for a single pooled effect estimate. The aim was therefore explanatory integration and critical comparison rather than exhaustive quantitative synthesis. The review followed established principles for rigorous narrative reviewing by making the conceptual scope, information sources, search terms, eligibility logic and appraisal criteria explicit while retaining the flexibility required to connect evidence generated with different experimental systems (Green *et al.*, 2006). This design does not remove the need for transparent selection or critical appraisal; rather, it places greater responsibility on evidence-claim alignment and on distinguishing broad mechanistic conclusions from context-specific observations.

2.2 Information Sources

Live searches were conducted in PubMed, Europe PMC, AGRIS, OpenAlex, OpenAIRE, the Directory of Open Access Journals (DOAJ) and Semantic Scholar. Searches were supplemented by backward and forward citation chasing from influential primary papers and recent reviews, related-article searching and checks of DOI landing pages and bibliographic records. PubMed and Europe PMC were particularly useful for molecular, physiological and chronobiological literature; AGRIS strengthened coverage of crop and horticultural evidence; and the multidisciplinary indexes broadened retrieval across plant science, agriculture and controlled-environment research. Only sources whose bibliographic identity could be verified were cited.

2.3 Search Strategy and Search Period

Searches focused on literature published from 1 January 2000 to 15 June 2026, while earlier seminal studies were retained when they established concepts that remain necessary for interpreting current evidence. Search concepts combined terms for the light environment with mechanisms and developmental outcomes. Representative strings included combinations such as “plant AND (light intensity OR daily light integral OR spectrum OR red far-red OR blue light) AND (growth OR morphology OR photosynthesis OR development)”; “plant AND (phytochrome OR cryptochrome OR phototropin OR UVR8) AND signalling”; “plant AND (circadian OR photoperiod) AND (flowering OR floral induction OR florigen)”; and “LED AND plant AND (photomorphogenesis OR flowering OR controlled environment)”. Crop-specific searches combined “photoperiod” or “flowering time” with rice, wheat, barley and other major species. Search terms were iteratively refined when key mechanistic papers used gene or protein names not captured by broad terminology.

2.4 Eligibility Criteria

Eligible sources were peer-reviewed original studies and high-quality reviews directly relevant to light perception, photosynthetic light use, photomorphogenesis, developmental plasticity, circadian entrainment, photoperiodic flowering or controlled-environment translation. Mechanistic studies in *A. thaliana* were included when they established receptor or signalling functions, while crop studies were prioritised for evaluating evolutionary divergence, agronomic relevance and external validity. Studies of isolated biochemical processes were included only when they materially clarified whole-plant light responses. Articles were excluded when the plant-light relationship was peripheral, bibliographic identity or DOI could not be verified, the source was retracted or methodologically unsuitable for the claim under consideration, or only a non-peer-reviewed version was available despite an accessible peer-reviewed record. English-language literature formed the principal evidence base.

2.5 Screening, Duplicate Handling and Study Selection

Records were screened first for topical relevance from titles and abstracts and then, where necessary, against full-text or detailed bibliographic and abstract records. Duplicate items retrieved across indexes were consolidated using combinations of title, author, year and DOI. Selection was purposive rather than frequency based: influential studies were retained because they established

mechanisms, provided strong replication or scale, corrected earlier assumptions, demonstrated crop divergence or exposed methodological limitations. Recent reviews were used to identify conceptual gaps and to locate foundational primary studies, but they did not substitute for direct verification of key claims. No screening counts are reported because this was not a systematic review with a prospectively fixed record set.

2.6 Critical Appraisal and Evidence Synthesis

Evidence was appraised according to experimental design, control of photon dose and spectrum, developmental stage, genetic validation, replication, measurement validity, ecological or agronomic realism and consistency with independent findings. Particular attention was given to confounding between spectral composition and total photon input, use of monochromatic versus broad spectra, single-leaf versus whole-canopy measurements, short-term versus developmental responses and model-to-crop extrapolation. Mechanistic confidence was considered highest when genetic perturbation, biochemical interaction and physiological phenotype converged. Crop-lighting claims were treated more cautiously when based on single cultivars, short growth cycles or conditions in which DLI, temperature or background light differed among treatments. Thematic synthesis was organised around dimensions of the light environment, receptor and signalling integration, vegetative development, photosynthetic acclimation, circadian organisation, flowering and controlled-environment application.

3. Light as a Multidimensional Developmental Environment

The biological meaning of light depends on more than the number of photons incident on a leaf. Photon quantity determines the potential rate of photosynthetic energy capture, but plant form and developmental timing depend strongly on how that quantity is distributed across wavelengths, time and space. DLI integrates photosynthetic photon flux density over a day and is often a better predictor of cumulative growth than an instantaneous irradiance measurement. Across a large meta-analytic dataset, many anatomical, physiological and reproductive traits changed systematically with DLI, although the shapes and saturation points of response curves differed among traits and plant functional groups (Poorter *et al.*, 2019). This result supports the use of DLI for comparing production environments, but it also shows why a single “optimal light intensity” is biologically implausible: optimality varies by trait, developmental stage and species.

Spectral quality carries a different class of information. Chlorophyll absorption contributes strongly to the efficiency with which photons drive photosynthesis, whereas photoreceptors use wavelength composition to infer environmental state. Red and far-red photons interconvert phytochrome between signalling states, allowing plants to detect both direct illumination and the spectral signature of neighbouring vegetation. Blue light activates cryptochromes and phototropins and contributes to stomatal opening, phototropism, chloroplast movement and suppression of excessive elongation. Ultraviolet-B can act as a damaging stressor at high exposure, yet at ecologically relevant doses it is also a signal sensed by UVR8 that modifies protective metabolism and development (Christie, 2007; Jenkins, 2014; Paik & Huq, 2019). Wavelength therefore cannot be interpreted solely through pigment absorption or solely through receptor action; the two systems operate simultaneously.

Photoperiod adds a temporal dimension that is not reducible to total daily photons. Two environments can supply the same DLI but differ markedly in day length, irradiance profile and twilight transitions. Such regimes can produce similar cumulative carbon input while delivering different information to the circadian and flowering systems. In photoperiodic species, the timing of light relative to circadian phase determines whether flowering regulators are stabilised or degraded and whether florigenic genes are expressed (Gendron & Staiger, 2023; Song *et al.*, 2015). This distinction is particularly important in controlled environments where day length and DLI can be altered independently.

Direction and spatial distribution also shape development. Phototropins permit directional blue-light sensing and can redirect organ growth towards favourable illumination, while within canopies the red-to-far-red ratio and blue-light availability decline before total irradiance becomes severely limiting. This enables anticipatory shade avoidance. Conversely, green and far-red photons penetrate leaves and canopies more deeply than strongly absorbed red and blue photons, meaning that the spectral composition experienced by lower tissues differs from the incident spectrum above a canopy (Terashima *et al.*, 2009; Zhen & Bugbee, 2020). A chamber experiment using a uniform top light therefore simplifies a naturally heterogeneous radiation field.

Temporal fluctuation is an additional and frequently neglected axis. Sunflecks, moving clouds, canopy motion and diurnal solar geometry generate changes over seconds to hours. Photosynthetic induction, stomatal kinetics, non-photochemical quenching and developmental signalling do not all respond on the same timescale. Reviews of fluctuating-light acclimation indicate that experimental waveforms are often slower or simpler than field fluctuations, weakening direct ecological extrapolation (Morales & Kaiser, 2020). The same problem applies to photoreceptor studies based on abrupt light pulses: they are powerful for mechanism discovery but do not necessarily predict the response to gradual dawn, dusk or intermittent shade.

Table 1 summarises these interacting dimensions. The central implication is that experiments should report photon quantity, spectrum, timing and spatial context together rather than treating one manipulated variable as if it were isolated from the rest of the light environment. This requirement becomes increasingly important when studies are compared across growth chambers, greenhouses and fields.

Table 1. Principal dimensions of the plant light environment and their developmental interpretation

Light dimension	Common descriptor	Principal biological information or constraint	Major developmental consequences	Key interpretive limitation	Supporting references
Photon quantity	Photosynthetic photon flux density; daily light integral	Energy available for photosynthesis and cumulative carbon gain	Biomass accumulation, leaf thickness, allocation, reproductive capacity	Instantaneous irradiance does not capture duration; trait-specific saturation differs	(McCree, 1971; Poorter *et al.*, 2019)
Spectral quality	Photon distribution by wavelength; blue, red, green, UV-B fractions	Simultaneous control of photosynthetic excitation and wavelength-specific receptor activation	De-etiolation, stomatal responses, leaf morphology, protective metabolism	Spectral treatments can change absorptance, photon dose and tissue temperature	(Christie, 2007; Hogewoning *et al.*, 2010; Jenkins, 2014)
Red-to-far-red balance	R:FR ratio; phytochrome photoequilibrium	Proximity of competing vegetation and open-canopy status	Internode/petiole elongation, leaf positioning, resource allocation, flowering shifts	Morphological responses depend on background irradiance, temperature and genotype	(Casal, 2013; Cheng *et al.*, 2021)
Photoperiod and light timing	Hours of light per 24 h; dawn/dusk phase	Seasonal and circadian information	Circadian entrainment, floral induction, growth rhythms	Equal daily photons can produce different temporal signals	(Gendron & Staiger, 2023; Greenham & McClung, 2015; Song *et al.*, 2015)
Direction and spatial distribution	Light vector, canopy penetration, within-canopy gradient	Direction of resource opportunity and neighbourhood geometry	Phototropism, chloroplast positioning, canopy architecture	Flat top-lighting poorly represents natural spatial heterogeneity	(Christie, 2007; Terashima *et al.*, 2009)
Temporal fluctuation	Frequency and amplitude of irradiance change	Dynamic resource availability and environmental variability	Photosynthetic induction, acclimation, growth timing	Laboratory fluctuations are commonly less complex than field patterns	(Morales & Kaiser, 2020; Nozue *et al.*, 2007)

Note. DLI = daily light integral; R:FR = red-to-far-red ratio; UV-B = ultraviolet-B

4. Photoreceptors and the Core Signal-Integration Network

4.1 Phytochromes: Red/Far-Red Sensing, Shade and Thermal Integration

Phytochromes are bilin-containing photoreceptors whose reversible photochemistry allows red and far-red radiation to alter the relative abundance of signalling-active states. This architecture underlies classic red/far-red reversibility but also provides a mechanism for continuous assessment of canopy spectral quality. In *A. thaliana*, phytochrome B (phyB) has a major role in restraining elongation under red-rich light. When the red-to-far-red ratio falls, as occurs after transmission or reflection by foliage, reduced phytochrome activity permits PIF accumulation and activation of elongation programmes (Casal, 2013; Cheng *et al.*, 2021). The phenotype is adaptive when elongation improves access to light, but it can be costly in crops because carbon and mechanical support are diverted away from harvestable organs.

The PIF family exemplifies how a receptor signal is converted into developmental reprogramming. Light-activated phytochromes bind selected PIFs and promote their inactivation or degradation, whereas darkness or shade allows PIF-dependent transcriptional programmes to dominate. PIFs integrate signals from phytochromes with hormone pathways, the circadian system and temperature, making them better understood as systems integrators than as simple downstream targets (Leivar & Monte, 2014). This interpretation is supported by evidence that elongation responses to shade involve rapid auxin biosynthesis and transport, and that gibberellin-dependent DELLA proteins interact with PIF-controlled growth (de Lucas *et al.*, 2008; Tao *et al.*, 2008).

A major conceptual advance has been recognition that phyB is also temperature sensitive. In warm conditions, the active phyB state reverts more rapidly towards the inactive state, providing a molecular route through which temperature and light converge on PIF-regulated growth. Independent studies using *A. thaliana* demonstrated phytochrome-dependent thermosensory effects on architecture and development (Jung *et al.*, 2016; Legris *et al.*, 2016). These findings weaken any interpretation of shade or far-red experiments that ignores leaf and ambient temperature. A treatment nominally designed to alter spectrum may also alter radiant heating, while a temperature treatment may change the effective state of the same receptor system.

4.2 Cryptochromes and Blue-Light Integration

Cryptochromes absorb mainly blue and ultraviolet-A radiation and regulate seedling photomorphogenesis, circadian entrainment and flowering. Their actions overlap extensively with phytochrome pathways. Under limiting blue light, cryptochromes can interact directly with PIF proteins, providing a molecular explanation for the strong elongation often observed when blue photons are depleted even if total photon flux remains substantial (Pedmale *et al.*, 2016). Competition experiments in which red-to-far-red and blue-light signals were manipulated together further demonstrate that plant architecture reflects receptor co-action rather than a single spectral ratio (de Wit *et al.*, 2016).

This cross-talk has practical implications. Broad-spectrum sunlight changes in multiple wavelength regions as leaves overlap, and artificial spectra designed around a high red fraction can unintentionally reduce cryptochrome activation. The resulting elongation may be useful for some ornamentals or leaf expansion but undesirable for compact seedlings. Because cryptochromes also interact with circadian and flowering networks, vegetative morphology and reproductive timing cannot always be optimised independently by spectral manipulation.

4.3 Phototropins and Directional Light Responses

Phototropins are blue-light receptor kinases that mediate phototropism, chloroplast relocation and stomatal responses, among other processes (Christie, 2007). Their importance is sometimes underrepresented in discussions of "light quality" that focus on red-versus-blue biomass effects. Directional sensing is essential in natural and greenhouse environments because plants are not exposed to spatially uniform radiation. Phototropism changes organ orientation and therefore future light interception; chloroplast movement modifies internal light absorption and photoprotection; and stomatal responses affect the coupling between photon supply and carbon dioxide uptake. These processes can change apparent photosynthetic efficiency without any alteration in the core photochemistry of the photosystems.

The phototropin literature also illustrates a general methodological point: molecular specificity does not imply isolated physiological effects. A blue-light treatment simultaneously changes phototropin, cryptochrome and photosynthetic excitation. Assigning a whole-plant response to one receptor therefore requires receptor mutants, biochemical evidence or other causal perturbations rather than spectral correlation alone.

4.4 UVR8 and Ultraviolet-B as Signal and Stress

UVR8 provides a distinct mechanism of ultraviolet-B perception. Structural and genetic work established that UVR8 undergoes light-dependent changes initiated by tryptophan-mediated UV-B absorption and then engages signalling components including COP1 (Rizzini *et al.*, 2011). Subsequent synthesis has clarified how UVR8-dependent signalling promotes acclimatory and protective responses while interacting with broader photomorphogenic networks (Jenkins, 2014; Podolec *et al.*, 2021). This duality is important: ultraviolet-B can be damaging at high doses, yet its signalling role at lower doses means that exclusion of ultraviolet radiation from protected cultivation may alter morphology and secondary metabolism even when photosynthetically active photon flux is unchanged.

Confidence in the existence and molecular identity of UVR8 signalling is high because structural, biochemical and genetic evidence converge. Confidence is lower when broad horticultural claims are made about an "optimal UV-B dose", because outcomes depend on species, developmental stage, dose rate, background light and the balance between signalling and damage. This is a recurring theme across photobiology: receptor mechanism may be conserved while dose-response relationships remain strongly contextual.

4.5 COP1–HY5–PIF Convergence and Network Logic

Photoreceptor pathways converge on a smaller set of transcriptional and proteostatic regulators. COP1 functions as a central repressor of photomorphogenesis in darkness, whereas light promotes conditions that permit positive regulators such as HY5 to accumulate. PIFs tend to promote dark- or shade-associated growth programmes, while HY5 contributes to light-responsive transcription and photomorphogenic development. The resulting network is not a simple binary switch. Different receptors change the abundance, localisation or activity of these regulators with different kinetics, and hormone and clock pathways alter the developmental consequences of a given light signal (Chen *et al.*, 2004; Leivar & Monte, 2014; Paik & Huq, 2019).

Table 2 highlights the functional specialisation of major receptor systems and, equally importantly, the extent to which their outputs overlap. The strongest mechanistic evidence comes from *A. thaliana*, where genetics, protein interactions and transcriptomic responses can be combined. Translation to crops is credible at the level of receptor classes and conserved signalling motifs, but the quantitative contribution of individual paralogues and downstream targets often differs after genome duplication and domestication.

Table 2. Major plant photoreceptor systems and their principal developmental functions

Photoreceptor system	Dominant spectral sensitivity	Representative downstream interactions	Established developmental roles	Important uncertainty in translation	Supporting references
Phytochromes	Red and far-red	PIF regulation; interaction with hormone and clock networks	De-etiolation, shade avoidance, architecture, flowering; phyB also integrates temperature	Relative roles of phytochrome paralogues and response thresholds vary among crops	(Casal, 2013; Cheng *et al.*, 2021; Jung *et al.*, 2016; Legris *et al.*, 2016)
Cryptochromes	Blue and UV-A	PIF interaction; COP1-related regulation; clock/flowering pathways	Suppression of elongation, photomorphogenesis, circadian entrainment, flowering	Responses depend strongly on background spectrum and blue photon dose	(de Wit *et al.*, 2016; Paik & Huq, 2019; Pedmale *et al.*, 2016)
Phototropins	Blue	Receptor kinase signalling controlling directional and cellular responses	Phototropism, chloroplast relocation, stomatal responses	Whole-plant growth effects can be indirect through altered light interception and gas exchange	(Christie, 2007)
UVR8	UV-B	COP1 and HY5-centred photomorphogenic signalling	UV-B acclimation, protective metabolism, developmental modulation	Signal-versus-damage balance is dose-, species- and background-light dependent	(Jenkins, 2014; Podolec *et al.*, 2021; Rizzini *et al.*, 2011)
COP1/HY5/PIF regulatory hub	Integrates multiple receptor inputs	Protein stability, transcriptional control and hormone cross-talk	Coordinates de-etiolation, organ growth and environmental plasticity	Network topology is conserved more strongly than quantitative phenotypic output	(Chen *et al.*, 2004; Leivar & Monte, 2014; Paik & Huq, 2019)

Note. COP1 = CONSTITUTIVELY PHOTOMORPHOGENIC 1; HY5 = ELONGATED HYPOCOTYL 5; PIF = PHYTOCHROME-INTERACTING FACTOR; UV-A = ultraviolet-A; UV-B = ultraviolet-B; UVR8 = UV RESISTANCE LOCUS 8

5. Vegetative Growth and Development: From Emergence to Canopy Competition

5.1 De-Etiolation as a Coordinated Developmental Transition

The transition from darkness to light after seedling emergence provides the clearest demonstration that light is developmental information rather than merely photosynthetic energy. Dark-grown angiosperm seedlings typically display elongation-oriented skotomorphogenesis, with an extended hypocotyl, an apical hook and poorly differentiated photosynthetic tissue. Illumination activates photoreceptors and rapidly shifts the developmental programme towards photomorphogenesis: hypocotyl elongation is restrained, cotyledons expand, chloroplast development proceeds and light-responsive transcription is reorganised (Chen *et al.*, 2004; Paik & Huq, 2019). These changes can occur before photosynthetic carbon gain becomes the dominant driver of growth, which is strong evidence that the initial response is informational.

The mechanistic architecture of de-etiolation is unusually well supported because receptor mutants, signalling mutants and direct protein interactions converge on the same regulatory logic. Light-dependent reduction of PIF activity and relief from COP1-mediated repression permit photomorphogenic regulators to act. Yet even in this tractable system, "light response" comprises parallel processes with different thresholds. Very low photon exposures may be sufficient for some phytochrome responses, while sustained irradiance is required for chloroplast development and later biomass accumulation. Consequently, short pulse experiments are powerful for identifying signalling causality but should not be used alone to infer long-term growth under agricultural illumination.

5.2 Shade Avoidance and the Cost of Competitive Architecture

Vegetation changes the spectrum before it dramatically reduces the total number of photons available. Chlorophyll preferentially absorbs red and blue radiation while reflecting or transmitting a larger fraction of far-red, generating a lower red-to-far-red ratio near neighbouring plants. Phytochromes therefore provide an early warning of competition. In shade-avoiding species, this signal promotes elongation of hypocotyls, stems or petioles, changes leaf angle and can accelerate flowering (Casal, 2013). The physiological logic is clear: reallocating growth towards vertical or lateral escape may improve future access to light.

The cost is equally important. Elongation requires carbon and structural investment and can reduce stem strength, leaf thickness or allocation to storage and reproductive tissues. In dense crop stands, a response that is adaptive for individual competitive success can be maladaptive for population yield. This distinction between individual fitness and crop productivity is one reason that the mechanistic shade-avoidance literature cannot be translated directly into management prescriptions. Breeding for reduced shade avoidance may increase harvest index or lodging resistance in some systems, but excessive suppression can impair canopy positioning or competitiveness against weeds.

Auxin provides a key link between spectral perception and growth execution. Low red-to-far-red conditions can stimulate rapid auxin biosynthesis, and altered auxin distribution promotes elongation in responsive tissues (Tao *et al.*, 2008). Gibberellin signalling contributes through DELLA proteins and their interaction with PIF-dependent growth regulation. Molecular studies showed that light and gibberellin pathways converge on the control of cell elongation rather than operating as independent inputs (de Lucas *et al.*, 2008; Feng *et al.*, 2008). These findings explain why shade responses vary with nutritional status, temperature and developmental stage: the photoreceptor signal enters a growth-regulatory system whose hormonal state is already context dependent.

5.3 Blue-Light Depletion and Multi-Receptor Competition Sensing

Natural shade does more than decrease red-to-far-red ratio. Blue photons are also depleted under foliage, and cryptochrome signalling contributes to elongation responses under limiting blue light. Direct interaction between cryptochromes and PIFs offers a mechanistic bridge between blue-light perception and growth, while experiments manipulating multiple spectral cues show that phytochrome and cryptochrome information is integrated during competition (de Wit *et al.*, 2016; Pedmale *et al.*, 2016). This is an important correction to the common practice of equating shade solely with red-to-far-red ratio.

The practical implication is that artificial “shade” treatments using only far-red supplementation may reproduce only part of the natural cue set. Likewise, neutral-density shade that lowers photon flux without changing spectrum tests energy limitation more than neighbour detection. Both experimental strategies are useful, but they answer different biological questions. Studies that compare their results without recognising this distinction can create apparent disagreement where the underlying treatments were not physiologically equivalent.

5.4 Light Direction, Organ Positioning and Developmental Feedback

Phototropism introduces a feedback loop in which perception changes the future light environment of the organ. Blue-light gradients sensed by phototropins lead to differential growth that reorients shoots and leaves. Chloroplast relocation and stomatal responses act on shorter timescales, modifying absorption and carbon dioxide supply (Christie, 2007). These responses are difficult to separate from photosynthetic effects at whole-plant scale because changing orientation changes both the quantity and spectral distribution of intercepted radiation.

This feedback is particularly relevant for protected cultivation. Vertical farms commonly use planar, spatially regular lighting, whereas field plants experience moving sun angles, self-shading and diffuse radiation. A phenotype selected under uniform top lighting may not preserve the same advantage under side lighting or a heterogeneous canopy. Conversely, interlighting in greenhouses can alter canopy light distribution without necessarily changing total incident photons, potentially improving use of lower leaves. Such effects are better interpreted through three-dimensional light interception than through fixture spectrum alone.

5.5 Temperature as a Modifier of Light-Dependent Architecture

The discovery that phyB can act as a thermosensory component demonstrates that light-dependent architecture cannot be analysed independently from temperature. Warm conditions can reduce the pool of active phyB and thereby promote PIF-mediated elongation responses that resemble aspects of shade avoidance (Jung *et al.*, 2016; Legris *et al.*, 2016). This convergence is biologically sensible because both vegetation shade and warm temperatures can signal environments in which altered organ positioning may improve performance. It also complicates experimental interpretation.

LED studies are sometimes described as purely spectral because light-emitting diodes produce less radiant heat than older lamps, but plant temperature can still differ because fixture distance, air movement, transpiration and total absorbed radiation differ among treatments. If elongation changes, a photoreceptor explanation is plausible only when thermal conditions are measured rather than assumed. More broadly, future climate conditions may change the same PIF-centred growth network through simultaneous shifts in temperature, canopy structure and light quality, so factorial rather than single-factor experiments are needed.

6. Light Quantity, Spectral Quality and Photosynthetic Acclimation

6.1 Photon Dose and Developmental Acclimation

Long-term growth responses to irradiance are not proportional to photon flux across the full range of natural or horticultural conditions. At low irradiance, additional photons commonly increase carbon gain and growth, but physiological and morphological traits approach saturation at different rates. The broad meta-analysis by Poorter *et al.* (2019) is especially informative because it aggregated responses across hundreds of experiments and many species, showing coordinated but trait-specific changes in leaf structure, photosynthetic capacity, allocation and reproduction along DLI gradients. Its strength lies in breadth and the use of continuous dose-response relationships rather than binary "high" and "low" categories. Its limitation is unavoidable heterogeneity: species, temperature, nutrient status, spectral composition and experimental duration varied substantially among contributing studies.

Acclimation involves structural as well as biochemical change. Leaves formed in high light are often thicker and support greater photosynthetic capacity per unit area, whereas shade leaves tend to invest in greater light capture per unit biomass. These differences mean that short-term gas-exchange measurements after transferring a leaf between light environments do not represent the phenotype that would have developed under the new regime. The distinction between instantaneous response and developmental acclimation is critical when interpreting growth-chamber studies. Reviews of fluctuating irradiance likewise show that plants can acclimate to the temporal pattern of light, not merely to the mean photon dose (Morales & Kaiser, 2020).

Because DLI combines intensity and duration, it is useful for production comparisons but insufficient for developmental prediction. A 12-hour photoperiod at high irradiance and an 18-hour photoperiod at lower irradiance can deliver the same DLI, yet they differ in instantaneous photosynthetic saturation, circadian timing, stomatal dynamics and flowering cues. Therefore, DLI should be reported alongside photoperiod and irradiance profile rather than treated as a complete description of the light environment.

6.2 Why Simple Colour Rankings Fail

The historical emphasis on red and blue wavelengths reflects both chlorophyll absorption and the spectral output of efficient LEDs, but whole-plant responses cannot be ranked reliably by wavelength without specifying irradiance and background spectrum. In cucumber, increasing the fraction of blue light altered leaf photosynthetic capacity, morphology and chemical composition even when red and blue photons were combined within controlled treatments (Hogewoning *et al.*, 2010). Such results demonstrate a real developmental role for blue light, but they do not imply that a fixed blue percentage is universally optimal. Blue-light responses depend on receptor activation, stomatal behaviour, leaf thickness and species-specific architecture.

Green light illustrates the danger of extrapolating from pigment absorption. Green photons are less strongly absorbed near the surface of a leaf than red or blue photons, yet this allows deeper penetration. Under strong white background light, green radiation can drive photosynthesis efficiently in deeper tissues because more strongly absorbed wavelengths become saturated nearer the surface (Terashima *et al.*, 2009). Measurements in lettuce further showed that the relative quantum yield of blue, green and red photons changes with light intensity, partly because absorption and non-photosynthetic energy costs differ among wavelengths (Liu & van Iersel, 2021). Consequently, a low absorptance at the leaf surface does not equate to low usefulness at high irradiance or within dense canopies.

Far-red radiation has prompted a similar re-evaluation. It was traditionally placed outside the 400–700 nm definition of photosynthetically active radiation, in part because far-red photons alone are inefficient at driving balanced excitation of the two photosystems. When delivered together with shorter wavelengths, however, far-red photons can participate in synergistic photosynthesis. Whole-canopy experiments found that far-red photons can contribute to carbon fixation with efficiencies comparable to traditionally defined photosynthetic photons under mixed spectra (Zhen & Bugbee, 2020). This evidence has substantial implications for lighting metrics and canopy design, but it should not be interpreted as meaning that far-red is interchangeable with visible photons in all proportions. A high far-red fraction also shifts phytochrome signalling and morphology, so energetic and signalling effects occur simultaneously.

6.3 Leaf-Scale Action Spectra Versus Canopy Performance

McCree's action-spectrum measurements remain foundational because they quantified the wavelength dependence of photosynthetic quantum yield across crop species (McCree, 1971). Their enduring value is methodological as much as numerical: wavelength effects were considered in relation to absorptance and photosynthetic response. Yet leaf-scale action spectra do not directly determine the optimum spectrum for a crop canopy. A wavelength that is absorbed very efficiently in the top leaf may produce high leaf-level response but poor penetration to shaded lower leaves. A less strongly absorbed wavelength may distribute excitation more evenly through the canopy.

This scale dependence helps reconcile apparently contradictory findings. Red photons are highly efficient for photosynthesis in many leaf-level measurements and are energetically economical to generate with LEDs. Green and far-red photons, however, can improve penetration and whole-canopy utilisation. The relevant unit for production is therefore not only quantum yield in an isolated leaf but carbon gain per incident photon across all photosynthetically active tissues over time. Morphological changes add another layer: far-red can expand leaf area and alter stem elongation, changing future interception of all wavelengths. A spectrum that initially appears physiologically inefficient can indirectly increase canopy photon capture through development.

6.4 Excess Light, Fluctuation and the Cost of Dynamic Mismatch

When absorbed energy exceeds the capacity for carbon assimilation and safe dissipation, photoprotective mechanisms become essential. The present review does not attempt a full account of photoinhibition, but high-light responses matter because growth is maximised by useful photon capture rather than by photon exposure per se. Under natural conditions, light fluctuates faster than stomata, carbon metabolism and photoprotective relaxation can always follow. Morales and Kaiser (2020) emphasised that the time structure of experimental light fluctuations often differs from the field, where sunflecks and clouds can generate rapid transitions. This methodological mismatch may overestimate the ability of plants to acclimate to dynamic light.

The problem has direct breeding and engineering implications. Improving steady-state photosynthetic capacity is not necessarily equivalent to improving carbon gain under fluctuating canopies. Similarly, lighting systems that maintain a constant photon flux may simplify control but miss opportunities to coordinate photon delivery with photosynthetic induction and circadian physiology. The evidence base for dynamic optimisation remains less mature than that for steady-state intensity or spectrum, and controlled experiments should not be mistaken for demonstrated production advantages until whole-cycle biomass or yield is measured.

Table 3 contrasts representative evidence that has changed how spectral and intensity effects are interpreted. Collectively, these studies support a shift from colour-ranking towards context-dependent photon management. They also show why mechanistic conclusions are strongest when photon dose, absorptance, developmental history and measurement scale are reported explicitly.

Table 3. Representative evidence on photon quantity, spectrum and photosynthetic development

Evidence domain	Experimental contribution	Principal inference	Methodological strength	Main limitation for generalisation	Supporting references
Broad DLI response	Meta-analysis across many traits and species	Growth, physiology and reproduction show trait-specific saturating responses to DLI	Large cross-species evidence base and continuous dose-response analysis	Heterogeneous species, spectra and co-environmental conditions	(Poorter *et al.*, 2019)
Blue-light dose response	Cucumber grown under controlled red/blue combinations	Blue photons alter photosynthetic capacity, morphology and composition beyond simple carbon supply	Controlled spectral treatments with integrated physiology	Species-specific; artificial spectrum and chamber context	(Hogewoning *et al.*, 2010)
Green-light penetration	Leaf photosynthesis under strong white background illumination	Green photons can support deeper-tissue photosynthesis efficiently under high irradiance	Mechanistic link between tissue optics and photosynthesis	Leaf-level findings do not alone predict whole-canopy yield	(Terashima *et al.*, 2009)
Intensity-dependent spectral efficiency	Lettuce gas exchange under blue, green and red light	Relative photon efficiency changes with irradiance and absorptance	Explicit separation of incident and absorbed-light effects	Short-term physiology in one crop does not establish developmental optimum	(Liu & van Iersel, 2021)
Far-red contribution	Mixed-spectrum canopy experiments	Far-red photons can contribute strongly to canopy carbon fixation when combined with shorter wavelengths	Whole-canopy carbon-gain perspective	Far-red also changes phytochrome signalling and morphology	(Zhen & Bugbee, 2020)
Fluctuating irradiance	Synthesis of dynamic-light acclimation studies	Mean irradiance alone does not capture photosynthetic performance under temporal variability	Integrates multiple response timescales	Laboratory fluctuations often do not reproduce field dynamics	(Morales & Kaiser, 2020)

Note. DLI = daily light integral

7. Circadian Entrainment and the Temporal Organisation of Growth

The circadian clock allows plants to anticipate predictable daily changes rather than simply react after light conditions change. Endogenous oscillators generate approximately 24-hour rhythms that are entrained by environmental cues, principally light and temperature. In plants, this temporal system regulates photosynthesis, carbohydrate metabolism, growth, hormone signalling and flowering, creating a framework in which the same light pulse can have different effects depending on when it occurs (Greenham & McClung, 2015; Nohales & Kay, 2016). Light therefore has a phase-setting function in addition to its energetic and photomorphogenic roles.

The adaptive value of circadian alignment is supported by experiments in which *A. thaliana* plants performed better when their internal circadian period matched the external day-night cycle. Matched plants showed advantages in photosynthesis, growth and competitive performance relative to mismatched conditions (Dodd *et al.*, 2005). This evidence is influential because it links molecular timing to whole-plant fitness rather than merely documenting rhythmic gene expression. Yet the result should not be simplified into the claim that a single clock period is universally optimal. Natural day length, temperature cycles and genotype interact, and crop breeding has repeatedly altered clock-associated genes during adaptation to latitude.

Growth rhythms reveal how circadian and environmental signals meet at the level of organ expansion. Nozue *et al.* (2007) showed that rhythmic hypocotyl growth can be explained by coincidence between internal timing and external cues, with PIF-related growth

capacity gated across the day. This mechanism is conceptually important because it demonstrates that the circadian system does not merely "turn growth on and off". Instead, it defines windows of sensitivity during which light and hormone signals have different consequences. Similar logic underlies photoperiodic flowering, where day length is measured through the phase relationship between clock-controlled regulators and illumination.

Photoreceptors contribute to entrainment, but the clock also modifies photoreceptor output. Cryptochromes and phytochromes influence phase and period, while clock-controlled expression changes the abundance or activity of signalling components. The direction of causality is therefore bidirectional: light resets the oscillator, and the oscillator gates the response to light. Experimental designs that compare treatments at only one clock time risk conflating a direct light effect with a phase effect. This is a particular concern when measuring transcription, stomatal conductance or metabolites that have large diel amplitudes.

The interaction between DLI and circadian timing further complicates controlled-environment optimisation. Extending the photoperiod at lower irradiance can preserve daily photon delivery while altering the phase and duration of light exposure. For some crops this can improve energy efficiency by allowing fixtures to operate at lower instantaneous power, but developmental effects may differ from those produced by a shorter, brighter day. In photoperiod-sensitive species, the same manipulation may trigger or delay flowering. Even in nominally day-neutral crops, clock-dependent carbon partitioning and starch turnover can change the efficiency with which a given DLI is converted into biomass.

A major weakness in translational studies is that circadian variables are often treated as background conditions rather than experimental factors. Light recipes may be compared without measuring whether clock phase, dawn transition or night interruption differs physiologically among treatments. This omission is especially problematic for dynamic LED systems capable of rapid spectral changes. The technology can produce precisely timed light cues, but the biological evidence needed to design circadian-aware schedules is less developed than the engineering capability. A strong next step is to combine clock reporter lines, crop phenology and whole-cycle carbon balance under lighting schedules that differ in temporal structure while holding DLI constant.

8. Photoperiodic Flowering: Conserved Logic and Crop-Specific Rewiring

8.1 The *Arabidopsis* Long-Day Framework

Photoperiodic flowering in *A. thaliana* is a model of external-coincidence timing. The circadian system controls the temporal pattern of CO expression, while light regulates CO protein stability and activity. Under inductive long days, a portion of CO expression occurs during light, permitting CO accumulation and activation of FT in leaf vascular tissue; under non-inductive short days, corresponding expression is largely confined to darkness, where CO is destabilised (Imaizumi & Kay, 2006; Song *et al.*, 2015; Valverde *et al.*, 2004). This mechanism converts day length into a molecular state without requiring a dedicated "day-length receptor".

The pathway is more elaborate than a simple clock-to-CO-to-FT chain. Blue-light sensing and the flavin-binding F-box protein FKF1 interact with GIGANTEA (GI) to regulate repressors of CO expression, helping establish the correct phase of CO activity. The timing of FKF1–GI complex formation is itself light dependent, providing a second layer of coincidence measurement (Sawa *et al.*, 2007). Later work showed that FKF1 also conveys timing information relevant to CO protein stabilisation (Song *et al.*, 2012). Phytochromes and cryptochromes then modify CO stability in a wavelength- and time-dependent manner. Photoperiodic flowering is therefore an emergent property of clock phase, receptor state and regulated protein turnover.

FT provides the connection between photoperiod perception in leaves and floral transition at the shoot apex. Genetic and grafting evidence established that FT-related florigenic activity is produced in leaves and participates in long-distance signalling, while the FT protein itself can move and contribute to floral induction (Corbesier *et al.*, 2007; Turck *et al.*, 2008). The strength of this conclusion is high because molecular genetics, expression data and transport experiments converge. What remains context dependent is how upstream environmental information controls FT-family genes in different species.

8.2 Why Photoperiodic Logic Cannot Be Transferred Unchanged to Crops

Rice provides the clearest demonstration of evolutionary rewiring. *Oryza sativa* is classically a facultative short-day species, and components homologous to the *Arabidopsis* photoperiod pathway can have different regulatory effects. Hd1, a CO homologue, promotes expression of the florigenic Hd3a pathway under short days but can repress flowering under long days, contributing to short-day behaviour (Hayama *et al.*, 2003). Rice also contains the B-type response regulator Ehd1, which promotes FT-like genes through a pathway with no direct equivalent in the canonical *Arabidopsis* long-day scheme. These features show that conserved gene families do not guarantee conserved regulatory sign.

Long-distance florigenic signalling is nevertheless broadly conserved. Hd3a protein acts as a mobile flowering signal in rice, paralleling the functional logic of FT in *Arabidopsis* (Tamaki *et al.*, 2007). This combination of conserved output and divergent upstream regulation is a useful general model for comparative photoperiodism. It explains why crop flowering networks often look familiar at the level of component names but behave differently under day-length treatments.

Temperate cereals provide another route to adaptation. In barley, natural variation in the pseudo-response regulator Ppd-H1 alters photoperiod responsiveness and contributes to adaptation across growing regions (Turner *et al.*, 2005). In wheat, photoperiod-insensitive Ppd-D1a alleles are associated with altered expression of a related pseudo-response regulator, enabling flowering under day lengths that would otherwise delay development (Beales *et al.*, 2007). These genes have major agronomic consequences because flowering time determines whether sensitive reproductive stages coincide with frost, heat or drought. Domestication and breeding have therefore repeatedly targeted photoperiod pathways, deliberately or indirectly, to expand geographic adaptation (Lin *et al.*, 2021).

The crop evidence warns against treating photoperiod sensitivity as a single binary trait. Alleles can alter the threshold, magnitude or phase of response rather than abolish light sensitivity entirely. Vernalisation, temperature, developmental age and stress can also modify flowering. A genotype described as photoperiod insensitive in one environment may still show day-length effects under another thermal regime. Accordingly, flowering studies need factorial environmental designs and precise genotype description rather than broad labels such as "long-day" or "short-day" as complete phenotypes.

8.3 Light Quality within Photoperiodic Signalling

Day length is measured through the spectral environment as well as through the presence or absence of photons. In *Arabidopsis*, photoreceptor-specific effects on CO stability mean that red, far-red and blue light delivered at the same clock time can have different consequences for flowering (Valverde *et al.*, 2004). This provides the mechanistic foundation for night-break lighting and end-of-day spectral treatments used in ornamental horticulture. Yet horticultural practice often extrapolates from a limited set of species, and the response can reverse between long-day and short-day plants.

The concept of "night interruption" also highlights a distinction between photosynthesis and signalling. A low-intensity photoperiodic light treatment can modify flowering without making a substantial contribution to DLI. Conversely, a high-DLI regime can fail to induce flowering if the timing of light is non-inductive. This separation is one of the clearest examples of why energy-based lighting metrics cannot substitute for photobiological understanding.

8.4 From Molecular Flowering Networks to Phenological Prediction

Mechanistic flowering genes have strong explanatory power in controlled environments, but prediction in the field remains more difficult. Natural dawn and dusk are gradual and spectrally dynamic, canopy shade changes photoreceptor state, and temperature alters both the circadian system and phytochrome kinetics. Genotypes also differ in vernalisation requirement, maturity genes and stress sensitivity. A molecular model that predicts flowering under constant chamber conditions may therefore explain only part of field phenology.

The most defensible cross-species conclusion is that florigen-like output signals are broadly conserved while the pathways linking photoperiod to those signals have diversified. Table 4 compares this pattern across representative species. This distinction is important for crop improvement: editing or selecting a conserved terminal flowering gene may have large pleiotropic effects, whereas tuning upstream photoperiod regulators can sometimes alter adaptation while preserving other developmental functions. Even so, pleiotropy remains a substantial risk because clock and photoreceptor components affect growth well beyond flowering.

Table 4. Conservation and divergence of representative photoperiodic flowering mechanisms

Species/ system	Photoperiodic tendency	Representative regulatory module	Conserved feature	Important divergence or agronomic implication	Supporting references
Arabidopsis thaliana	Long-day	Clock/FKF1–GI control of CO; light-dependent CO stability; FT induction	FT-family florigenic output and leaf-to-apex signalling	CO activity depends on coincidence between circadian phase and light	(Corbesier *et al.*, 2007; Sawa *et al.*, 2007; Song *et al.*, 2012, 2015; Valverde *et al.*, 2004)
Oryza sativa	Predominantly short-day	Hd1/Hd3a and Ehd1-dependent routes	Mobile FT-like florigenic signal	CO homologue Hd1 can promote or repress flowering according to day length; Ehd1 adds crop-specific control	(Hayama *et al.*, 2003; Tamaki *et al.*, 2007)
Hordeum vulgare	Long-day responsiveness varies by allele	Ppd-H1 pseudo-response regulator	Clock-associated photoperiod control	Natural allelic variation contributes to regional adaptation and heading time	(Turner *et al.*, 2005)
Triticum aestivum	Long-day, with photoperiod-insensitive breeding alleles	Ppd-D1-related pseudo-response regulation	Photoperiod pathway remains a major phenology determinant	Ppd-D1a misexpression reduces dependence on inductive photoperiod and alters adaptation	(Beales *et al.*, 2007)
Crop adaptation across species	Variable	Recurrent selection on photoperiod and flowering-time genes	Seasonal timing is repeatedly targeted during domestication	Similar gene families can be selected in different directions; pleiotropic effects depend on genetic background	(Lin *et al.*, 2021)

Note. CO = CONSTANS; Ehd1 = EARLY HEADING DATE 1; FKF1 = FLAVIN-BINDING, KELCH REPEAT, F-BOX 1; FT = FLOWERING LOCUS T; GI = GIGANTEA; Hd1 = HEADING DATE 1; Hd3a = HEADING DATE 3a; Ppd = photoperiod response locus

9. Translating Light Biology to Controlled-Environment Horticulture

9.1 LEDs as Experimental and Production Tools

Light-emitting diodes (LEDs) have transformed plant-light research because they permit independent control of spectral composition, photon flux, photoperiod and, increasingly, temporal waveform. Their value is therefore not merely that they can replace older lamps efficiently; they allow hypotheses derived from photoreceptor and photosynthetic biology to be tested with unprecedented precision. At the same time, the technological ability to create a spectrum does not establish that the spectrum is biologically optimal. Reviews of horticultural LED research consistently show strong species, cultivar and developmental-stage

dependence, together with wide variation in experimental background light, photon dose and duration (Bantis *et al.*, 2018; Paradiso & Proietti, 2022). The most reliable use of LEDs is consequently as controllable components of a complete environmental system, not as sources of universally transferable "light recipes".

Energy efficiency is an important constraint because photons are a major operating input in fully controlled production. The development of efficient solid-state lighting has made it possible to deliver high photon flux with less waste heat and to position fixtures close to crops, while spectral tunability permits light to be matched to physiological objectives (Pattison *et al.*, 2018). Yet fixture efficacy, measured as photons produced per unit electrical energy, is only one component of biological energy-use efficiency. A highly efficient fixture can still produce poor crop energy conversion if the spectrum drives excessive elongation, if photons are delivered when photosynthesis is saturated, or if canopy architecture leaves much of the radiation unabsorbed.

This distinction argues for a hierarchy of optimisation. The first requirement is adequate photon supply for the target crop and developmental stage. The second is an appropriate photoperiod and temporal distribution that avoid unwanted flowering or circadian mismatch. Spectral tuning can then refine morphology, stomatal behaviour, pigmentation or flowering. In many commercial situations, the gain from correcting inadequate DLI is likely to exceed the gain from small adjustments in spectral composition. This inference is consistent with the broad importance of DLI across plant traits (Poorter *et al.*, 2019) and with evidence that spectral effects often interact with irradiance (Liu & van Iersel, 2021).

9.2 Red and Blue Light: Useful Baseline, Incomplete Prescription

Red and blue LEDs became common in plant production because they align with chlorophyll absorption peaks, activate major photoreceptor systems and can be generated efficiently. Red-dominant spectra can support high photosynthetic rates, while inclusion of blue light helps regulate stomata, leaf morphology and compactness. Cucumber experiments demonstrated that blue-light fraction can substantially change photosynthetic capacity and anatomy even under comparable red-plus-blue treatments (Hogewoning *et al.*, 2010). These findings justify a role for blue photons beyond simple energy supply.

The weakness arises when a particular red:blue ratio is presented as generalisable. Crop species differ in leaf optical properties, receptor abundance and morphology; cultivars within a species can differ in compactness and flowering responses; and the optimum for transplant quality may differ from that for final biomass or nutritional composition. Blue light can also reduce leaf expansion or increase investment in protective metabolism, so a response that improves leaf-level photosynthetic capacity may not maximise total canopy area. A robust production strategy therefore requires the target outcome to be specified before spectral optimisation is attempted.

9.3 Green and Far-Red Photons in Canopy Design

Broad-spectrum or white-light systems reintroduced attention to green wavelengths, while far-red LEDs made it possible to manipulate both phytochrome signalling and deep-canopy photon distribution. The evidence reviewed in Section 6 shows that green photons can drive photosynthesis efficiently in deeper leaf tissues under strong background illumination and that far-red photons can contribute to canopy carbon gain when combined with shorter wavelengths (Terashima *et al.*, 2009; Zhen & Bugbee, 2020). These findings challenge the assumption that photons outside chlorophyll absorption maxima are intrinsically wasted.

Far-red is especially powerful because it changes both energy capture and morphology. Increasing far-red can promote leaf expansion and stem or petiole elongation through phytochrome signalling. In a dense canopy, greater leaf expansion may increase photon interception and thus biomass, but excessive elongation can reduce compactness, mechanical quality or harvest index. The direction of the production effect therefore depends on whether the morphological response improves the crop's spatial use of light. This is one reason that canopy-level experiments are more informative than short-term gas exchange when evaluating far-red supplementation.

9.4 Photoperiod and Flowering Control in Protected Crops

Controlled environments can decouple photoperiod from natural seasonality. This is particularly valuable for ornamental and seed crops in which flowering time determines marketability or production scheduling. Because photoperiodic signalling can be triggered by relatively low-intensity light at critical times, night interruption or day-extension lighting may change flowering with modest contribution to total DLI. The mechanistic basis lies in clock- and photoreceptor-dependent regulation of flowering pathways, although the effective wavelength and timing differ among species (Gendron & Staiger, 2023; Song *et al.*, 2015).

The risk is that flowering control is sometimes treated as an isolated switch. Photoperiod manipulations also alter circadian entrainment, carbohydrate turnover and the duration of photosynthetic activity. A long photoperiod at low instantaneous irradiance may improve electrical load management but may not be physiologically equivalent to a shorter, brighter day with the same DLI. For photoperiod-sensitive crops, it can also alter developmental duration, thereby changing the time available for leaf area development before reproduction. Production models should therefore integrate phenology and carbon gain rather than optimise them separately.

9.5 Dynamic and Stage-Specific Lighting

A major opportunity is to move from static recipes to stage-specific and dynamic lighting. Seedlings may benefit from spectra that restrain elongation and promote sturdy morphology, vegetative crops may benefit from spectra that maximise canopy interception,

and reproductive stages may require photoperiodic or spectral cues that coordinate flowering. Dynamic systems could also reduce photon supply during periods of transient photosynthetic limitation and increase it when the canopy can use additional light. Such strategies are biologically plausible, but direct evidence for whole-cycle energy savings and yield stability remains limited compared with evidence for static spectral treatments.

The strongest future approach is therefore adaptive rather than prescriptive. Sensors of canopy light interception, temperature and gas exchange can be combined with crop models and genotype-specific phenology to adjust lighting in real time. Yet adaptive control should be built on causal biology. An algorithm that optimises short-term carbon dioxide exchange without accounting for photomorphogenesis may inadvertently produce an undesirable canopy. Conversely, a spectrum chosen for compactness may reduce carbon gain. The relevant objective function must include final yield, quality, developmental timing and electrical energy use.

Table 5 summarises translational strategies and the confidence that can reasonably be placed in them. The evidence supports the principle of deliberate photon management, but not universal species-independent spectral recipes. The most defensible recommendations concern measurement discipline and matching light treatment to a defined developmental objective.

Table 5. Translation of light-response biology into controlled-environment strategies

Management objective	Light strategy	Mechanistic basis	Evidence-based opportunity	Principal risk or limitation	Supporting references
Increase biomass where light is limiting	Raise photon supply and DLI within crop-specific tolerance	Greater photosynthetic energy supply and developmental acclimation	Often produces large gains when baseline DLI is inadequate	Saturation, photoprotection costs and thermal/nutrient co-limitation	(Poorter *et al.*, 2019)
Control compactness and leaf form	Adjust blue fraction within an adequate background spectrum	Cryptochrome/phototropin signalling, stomatal and anatomical responses	Can restrain excessive elongation and alter leaf physiology	Response varies with species, cultivar, photon flux and developmental stage	(Hogewoning *et al.*, 2010; Pedmale *et al.*, 2016)
Improve canopy photon distribution	Include broad-spectrum green and context-appropriate far-red	Deeper optical penetration; far-red synergy with shorter wavelengths	May improve whole-canopy use of incident photons	Far-red simultaneously changes phytochrome signalling and architecture	(Terashima *et al.*, 2009; Zhen & Bugbee, 2020)
Schedule flowering	Day extension, night interruption or photoperiod manipulation	Circadian coincidence and photoreceptor regulation of flowering genes	Precise seasonal control in responsive crops and ornamentals	Direction and magnitude of response depend on photoperiodic class and genotype	(Gendron & Staiger, 2023; Song *et al.*, 2015; Valverde *et al.*, 2004)
Reduce energy use without compromising development	Match photon delivery to DLI target, canopy demand and efficient fixture operation	Integration of photosynthetic demand with lighting efficacy	Potential to reduce wasted photons and exploit temporal control	Short-term photosynthesis is an incomplete proxy for whole-cycle yield	(Pattison *et al.*, 2018; Paradiso & Proietti, 2022)
Optimise successive developmental stages	Change spectrum, intensity and timing across the crop cycle	Stage-dependent receptor sensitivity, architecture and flowering competence	Allows different objectives for propagation, vegetative growth and reproduction	Few studies validate complex recipes across full production cycles and cultivars	(Bantis *et al.*, 2018; Paradiso & Proietti, 2022)

Note. DLI = daily light integral

10. Cross-Cutting Methodological Constraints and Sources of Discordance

A major reason for disagreement in the plant-light literature is that different studies use the same verbal treatment labels for physically and biologically different environments. “Red light”, for example, may mean a narrow-band LED with no other photons, a red-enriched white spectrum or a treatment that differs from the control in both wavelength and total photon flux. “Shade” may mean a lower red-to-far-red ratio at constant photosynthetic photon flux, neutral-density reduction of irradiance, or actual vegetative shade in which multiple spectral regions and temperature change simultaneously. Without full spectral and photon reporting, comparison is uncertain even when the biological material is identical.

The most important confounder is photon dose. If spectral treatments are compared at equal electrical power rather than equal photon flux, differences in fixture efficacy can generate different numbers of photons. If treatments are equalised for photosynthetic photon flux density but one contains substantial far-red radiation beyond the conventional 400–700 nm range, total incident photons differ. Conversely, equal DLI does not equalise instantaneous irradiance or photoperiod. These choices are not inherently wrong, but the causal interpretation depends on which variable was held constant. The far-red literature makes this issue particularly visible because definitions of photosynthetically active photons affect both biological accounting and engineering efficacy (Zhen & Bugbee, 2020).

A second limitation is scale. Molecular studies often use seedlings, short light pulses and mutant backgrounds that maximise signal detection. Photosynthetic studies may use individual leaves over minutes, whereas horticultural studies assess biomass after weeks. Field phenology integrates months of variable light, temperature and water status. Agreement across these scales is strong evidence for general mechanism; disagreement does not necessarily mean one study is incorrect. For example, a wavelength may produce a high short-term quantum yield but a different whole-plant outcome because it changes leaf expansion, flowering time or canopy architecture. Critical synthesis must therefore avoid treating leaf gas exchange as a surrogate for yield unless that relationship is demonstrated.

A third problem is developmental stage. Photoreceptor abundance, leaf optical properties, source-sink relationships and competence to flower change over ontogeny. Seedling responses dominate the molecular photomorphogenesis literature because they are experimentally convenient, but adult architecture and reproductive timing involve additional regulatory layers. Likewise, a lighting treatment that improves transplant morphology may not maximise final production if maintained throughout the crop cycle. Stage-specific experiments are more informative than assuming temporal constancy of light response.

Genotype is another major source of heterogeneity. The mechanistic literature is heavily concentrated in *A. thaliana*, while applied studies often use a small number of commercial cultivars. Crop domestication has altered photoperiod and architecture genes, and breeding has selected different sensitivities to shade, temperature and day length (Beales *et al.*, 2007; Lin *et al.*, 2021; Turner *et al.*, 2005). Generalisation from one genotype is therefore particularly risky for flowering. Multi-genotype studies are also needed in controlled-environment horticulture because a lighting regime that appears optimal for one cultivar may simply compensate for that cultivar's particular architecture.

Temperature is frequently under-characterised. Phytochrome thermosensing provides a direct molecular reason to treat temperature as part of the light response, not merely as an unrelated environmental variable (Jung *et al.*, 2016; Legris *et al.*, 2016). Different fixtures can alter leaf energy balance, and differences in stomatal conductance under blue light can change transpirational cooling. Air temperature alone may therefore fail to capture physiologically relevant thermal differences. Leaf temperature and vapour pressure deficit should be measured where spectral treatments are expected to alter gas exchange or morphology.

Finally, many controlled-environment studies are short and statistically underpowered for production claims. Morphological differences can appear rapidly, while consequences for cumulative biomass, reproductive success or energy-use efficiency emerge later. Publication bias may also favour distinctive spectral effects over null results. Reviews of LED horticulture provide valuable coverage but inherit heterogeneity in fixture design, species and outcome definitions (Bantis *et al.*, 2018; Paradiso & Proietti, 2022). Stronger inference will require common reporting standards, preregistered primary outcomes in comparative production trials and replication across facilities and seasons.

11. Future Directions

The immediate priority is to replace one-dimensional descriptions of light with experimentally complete light environments. Studies should report spectral photon distributions, DLI, photoperiod, temporal waveform, fixture geometry and, where relevant, within-canopy profiles. This is not merely a reporting refinement. It is necessary to determine whether an observed response is attributable to receptor signalling, carbon supply, canopy penetration or a correlated physical change. Factorial designs that manipulate spectrum and photon dose independently are particularly valuable because many current conclusions about "colour effects" are based on treatments in which those dimensions covary. Where far-red is used, reporting both conventional photosynthetic photon flux and broader photon totals will make comparisons more interpretable.

A second priority is to connect molecular photoreceptor states with whole-canopy performance. The mechanistic understanding of phytochrome, cryptochrome and PIF networks is considerably more advanced than the ability to predict crop biomass or yield from those networks. Bridging experiments should combine photoreceptor or signalling genotypes with three-dimensional canopy imaging, intercepted radiation, gas exchange and final reproductive output. In crops with duplicated photoreceptor families, gene editing and near-isogenic lines can help distinguish paralogue-specific effects without assuming *Arabidopsis* equivalence. Such studies should be performed across planting densities because the value of shade avoidance depends on competition and canopy architecture.

A third priority is dynamic light biology. Natural irradiance varies over seconds, minutes and hours, while many chamber studies use step changes or constant light. Experiments should reproduce realistic fluctuation spectra and quantify not only steady-state photosynthesis but induction kinetics, stomatal responses, photoprotective relaxation and cumulative carbon gain (Morales & Kaiser, 2020). Dynamic-light research should also include the circadian dimension. Treatments with identical DLI but different timing can reveal whether photon delivery can be shifted towards phases of higher photosynthetic or developmental efficiency without creating clock misalignment.

Flowering research requires a more comparative and predictive framework. The *Arabidopsis* CO–FT model remains mechanistically powerful, but crop evidence shows substantial rewiring upstream of florigenic output (Gendron & Staiger, 2023; Hayama *et al.*, 2003; Turner *et al.*, 2005). Comparative studies should therefore focus on network function rather than homology alone. Multi-environment phenotyping of edited or naturally varying photoperiod alleles should measure flowering time, vegetative biomass, reproductive success and stress exposure across latitude-relevant day lengths and temperatures. This would clarify which alleles provide robust adaptation and which merely shift flowering under narrow chamber conditions.

Thermal-light integration deserves specific attention under climate change. Because phyB and PIF pathways respond to both spectral and thermal inputs, warming can alter the developmental meaning of a given red-to-far-red environment (Jung *et al.*, 2016; Legris *et al.*, 2016). Future studies should use factorial light-quality and temperature designs, ideally with measured leaf temperature, to determine whether breeding for reduced shade avoidance remains effective under warmer canopies. The same approach should be extended to flowering, where temperature modifies clock function and photoperiodic responsiveness.

Controlled-environment agriculture offers an unusually strong platform for causal testing because light can be manipulated independently of weather. The most informative production trials will move beyond fixed red-blue recipes to stage-specific and adaptive schedules. A rigorous design would compare a static reference treatment with dynamic schedules that maintain the same total electrical energy or DLI, then quantify whole-cycle yield, quality, flowering time and energy use. Such experiments should include multiple cultivars and be replicated across facilities to distinguish general mechanisms from installation-specific effects. Biological optimisation should be evaluated against electrical cost rather than yield alone.

Canopy-scale spectral modelling is another priority. Leaf action spectra and absorptance data should be integrated with three-dimensional ray tracing and developmental models so that changes in leaf angle, expansion and internode length feed back onto future photon interception. Green and far-red photons are especially important test cases because their value emerges partly through deeper penetration and morphology (Terashima *et al.*, 2009; Zhen & Bugbee, 2020). Models should be validated against measured whole-canopy carbon exchange and final biomass rather than inferred from optical simulations alone.

A longer-term need is predictive genotype-by-light modelling. Photoperiod genes, photoreceptor alleles and architectural traits could be combined with environmental data to forecast how cultivars respond to latitude, planting density, seasonal light and protected-culture regimes. This requires standard phenotyping across genotypes and environments and would benefit from shared datasets that include full spectral metadata. Machine-learning approaches may help identify interactions, but they should complement rather than replace mechanistic constraints; otherwise, models risk learning facility-specific correlations that fail outside the training environment.

Finally, future studies should separate production objectives. Maximising vegetative biomass, edible yield, nutritional quality, compactness, flowering uniformity and electrical energy efficiency are not identical goals. A spectrum that increases secondary metabolites may reduce leaf expansion; a treatment that accelerates flowering may shorten vegetative growth; and far-red that improves canopy interception may reduce compactness. Multi-objective experiments are therefore more informative than claims of a single optimum. The field will advance most rapidly when light treatments are evaluated against explicitly ranked biological and production outcomes and when uncertainty is reported as carefully as mean response.

12. Conclusions

Light regulates plants simultaneously as an energy source and as a structured environmental signal. The strongest evidence supports an integrated system in which photon quantity constrains carbon gain, while spectral quality, timing and direction are interpreted through photoreceptors and the circadian clock to reshape development. Phytochromes, cryptochromes, phototropins and UVR8 have distinct sensory properties but converge on shared regulatory nodes, particularly PIF-, COP1- and HY5-centred networks. These pathways coordinate de-etiolation, organ positioning, shade responses and hormone-dependent growth, and their outputs are further modified by temperature.

Photosynthetic evidence shows that simple rankings of wavelength are inadequate. Red and blue photons are highly useful, but green and far-red photons can contribute substantially when tissue depth, canopy penetration and mixed-spectrum excitation are considered. Spectral effects on whole-plant growth therefore emerge from both immediate photosynthetic efficiency and developmental changes in leaf area, anatomy and canopy architecture. DLI is a valuable measure of cumulative photon supply, but it cannot replace information about photoperiod, irradiance profile or spectrum.

Flowering demonstrates most clearly how light information is converted into developmental timing. The long-day *Arabidopsis* framework establishes a robust mechanism in which circadian phase and photoreceptor state regulate CO and FT, yet crop studies show that upstream photoperiodic networks have been extensively rewired. Conservation of florigen-like outputs coexists with substantial divergence in the genes that connect day length to those outputs. This limits direct transfer of model-species mechanisms but creates opportunities for crop adaptation through targeted modification of photoperiod sensitivity.

Controlled-environment agriculture can exploit these insights, but the evidence does not support universal spectral recipes. The most defensible approach is to define the production objective, provide an appropriate photon dose and photoperiod, and then use spectral and temporal control to refine morphology, flowering or canopy performance. Progress will depend on experiments that integrate molecular mechanisms with whole-canopy carbon gain, reproductive phenology and energy use under realistic dynamic environments.

13. Limitations

As a critical narrative review, this synthesis is intrinsically vulnerable to selection and interpretive bias despite a transparent search strategy, explicit eligibility criteria and critical appraisal. The evidence base is also heterogeneous in species, cultivar, developmental stage, light source, spectral definition, photon dose and outcome measurement, which limits direct comparison and precludes meaningful quantitative synthesis across the full topic. Mechanistic evidence is disproportionately derived from *Arabidopsis thaliana*, whereas applied lighting studies often involve a small number of horticultural cultivars under controlled

conditions. English-language and openly accessible bibliographic records were prioritised, so relevant evidence that was poorly indexed or inaccessible may have been missed. Publication bias towards statistically significant or visually distinctive spectral responses may also exaggerate the apparent consistency of some lighting effects. Finally, rapid development of LED systems, spectral measurement standards and crop genetic resources means that practical recommendations may evolve as better multi-genotype and whole-cycle studies become available.

Declaration of AI Use

This manuscript was prepared through the intellectual contributions of the author(s) to the study design, data analysis, interpretation of results, and scholarly content. Grammarly and ChatGPT were used solely to assist with grammatical refinement and reference formatting during manuscript revision. The author(s) accept full responsibility for the accuracy, integrity, and final content of the manuscript.

Competing Interests

Authors have declared that they have no known competing financial interests or non-financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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