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Hydroponic Cultivation as a Sustainable Platform for Plant Pigment Production: A Mechanistic Review of Nutrient and Light Regulation

Moaed Ali Al Meselmani*

Grantham Centre for Sustainable Futures, University of Sheffield, UK

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***Corresponding author:** Moaed Ali Al Meselmani, Grantham Centre for Sustainable Futures, University of Sheffield, Sheffield S10 2TN, UK

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Abstract

Field cultivation of pigment-rich crops for use as natural dyes and functional phytochemicals is constrained by seasonal and site variability, by the land and water demands of large-scale field production, and by the environmental and regulatory concerns increasingly attached to synthetic colorants. Controlled-environment hydroponic systems address these constraints directly: They decouple pigment production from soil and season and allow reproducible manipulation of the root-zone chemical environment as a lever on pigment biosynthesis. Anthocyanins, carotenoids, battalions, and chlorophylls are the four principal pigment families with established or emerging value as renewable colorants and functional phytochemicals. This review synthesizes verified evidence on how nitrogen, potassium, phosphorus, iron speciation, light quality, and bio stimulant inputs influence pigment accumulation in hydroponically grown crops, and integrates this with the transcriptional architecture, principally the MYB-bHLH-WD40 complex, the COP1-HY5 light-signaling hub, and phosphate-starvation signaling through PHR1, that governs these responses. Confirmed findings include a 461.7 percent increase in anthocyanin concentration in carrot microgreens treated with a legume-derived protein hydrolysate [1], genotype-dependent phenolic responses to nutrient solution strength in red versus green lettuce spanning approximately a five-fold decrease to an eleven-fold increase across phenolic subclasses [2], a direct molecular link between phosphate starvation and anthocyanin gene expression through PHR1 binding of F3'H and LDOX promoters [3], and engineering-scale anthocyanin enrichment in tomato through heterologous transcription factor expression [4]. This review is deliberately conservative: claims that could not be traced to a verifiable primary source have been removed rather than retained in qualified form, and the resulting evidence base, while narrower than is typical for reviews in this area, is intended to be fully reliable for downstream citation.

Keywords: Hydroponics; Natural dyes; Pigment biosynthesis; Nutrient management; Transcription factors; Anthocyanins; Carotenoids; Controlled-environment agriculture; Microgreens

Introduction

Synthetic colorants derived from petrochemical feedstocks remain dominant in food and textile applications, but their use faces increasing regulatory and consumer pressure. Several synthetic azo dyes have been linked to adverse health outcomes in controlled trials; a randomized, double-blind, placebo-controlled study found that certain artificial food colorings and additives increased hyperactive behavior in young children [5], and genotoxicity studies have reported DNA-damaging effects of specific synthetic colorants *in vitro* [6]. These findings have contributed to tightening regulatory scrutiny of synthetic colorants in several jurisdictions and rising consumer demand for naturally derived alternatives [7].

Beyond the toxicological concerns above, reliance on field-grown or wild-harvested plant biomass as the primary source of natural pigments carries its own sustainability costs: Pigment-rich crops compete with food production for arable land and water, and yield and pigment content vary with season, climate, and soil condition in ways that are difficult to control. These pressures motivate interest in production systems that can deliver pigment content reproducibly while reducing dependence on additional field acreage. The present review addresses one such system, hydroponic and other soilless cultivation, and specifically the nutrient-and light-based interventions by which pigment accumulation can be directed within it. Hydroponic systems decouple plant nutrition from soil, allowing continuous, quantifiable control over nutrient ion concentrations, pH, electrical conductivity, and, in systems designed for it, light spectrum and intensity [8].

Adjacent approaches to sustainable pigment supply, including green solvent extraction and plant cell, tissue, and organ culture, raise separate and substantial technical questions of their own and are outside the scope of the mechanistic, cultivation-stage evidence synthesized here. Plant pigments frequently carry bioactive value beyond color. Anthocyanins are associated with antioxidant and cardiovascular-protective properties in dietary and cell-based studies [9]. Carotenoids function as antioxidants and are essential dietary precursors for vitamin A and components of retinal photoprotection [10]. Betalains, restricted taxonomically to the order Caryophyllales, show antioxidant and free-radical-scavenging activity and have an established history of use as natural colorants, including in products derived from Opuntia and beet [11]. This combination of color and bioactivity creates a commercial case for production systems capable of delivering pigment content with consistency. Because several of the variable's controllable in hydroponic systems act as direct molecular signals engaging nutrient- and light-sensing pathways that converge on pigment biosynthesis gene networks, hydroponic systems are mechanistically well suited to pigment-directed crop management, not merely to consistent vegetative growth.

Biosynthetic Architecture of Plant Pigments

Anthocyanins and the MYB-bHLH-WD40 complex

Anthocyanins are water-soluble flavonoid glycosides responsible for red, purple, and blue coloration across most flowering plant lineages, with several hundred structural variants described, arising from differences in hydroxylation, glycosylation, and acylation patterns [12]. Biosynthesis proceeds through the general phenylpropanoid pathway, beginning with phenylalanine ammonia-lyase, abbreviated PAL [13], followed by chalcone synthase, chalcone isomerase, flavanone 3-hydroxylase, dihydroflavonol reductase, and anthocyanidin synthase, culminating in glycosylation and vacuolar transport [14,15]. Transcriptional control of this pathway is exercised principally by the MYB-bHLH-WD40 ternary complex, often abbreviated MBW, in which R2R3-MYB transcription factors provide target-gene specificity, basic helix-loop-helix proteins act as co-activators, and WD40 proteins serve a structural scaffolding role [16]. This complex is the convergence point for nutritional and light signals discussed in Sections 3 and 6.

Carotenoids, battalions, and chlorophylls

Carotenoids are C40 tetraterpenoid pigments synthesized in plastids via the methylerythritol phosphate pathway. Phytoene synthase catalysis the first committed and rate-limiting step; its transcription is suppressed in darkness by phytochrome-interacting factor transcription factors and de-repressed under light as red-light-activated phytochrome B promotes their degradation [17]. Betalains are nitrogen-containing, tyrosine-derived pigments confined to the plant order Caryophyllales [18]. Cytochrome P450 enzymes of the CYP76AD family convert tyrosine to L-DOPA, an essential and rate-limiting step toward betalain production; this was demonstrated directly through cloning and functional characterization of the beet R locus, which encodes a CYP76AD-family P450 required for red betalain pigmentation [19]. Subsequent tyrosine hydroxylation and DOPA dioxygenase activity together establish the shared betalamic acid chromophore from which both betacyanin's and betaxanthins derive [20]. Chlorophyll biosynthesis requires magnesium chelation into the porphyrin ring by the Mg-chelatase enzyme complex, a step for which adequate magnesium supply is a direct prerequisite [21].

Macronutrient Regulation of Pigment Biosynthesis

Nitrogen

Nitrogen status is the single most influential macronutrient variable affecting anthocyanin accumulation, acting through both transcriptional and metabolic flux mechanisms [22]. At the transcriptional level, members of the LBD transcription factor family, specifically LBD37, LBD38, and LBD39, function as direct repressors of anthocyanin biosynthetic genes under nitrate-replete conditions in Arabidopsis; their expression is induced by nitrate and they in turn repress genes including those encoding PAP1, also known as MYB75, the principal anthocyanin pathway activator [23]. Reducing nitrogen availability relieves this repression, increasing anthocyanin pathway gene expression, and this regulatory logic is consistent with the long-observed empirical pattern of anthocyanin accumulation under nitrogen-limited growth conditions across many species [22]. Genotype interacts strongly with this nitrogen response. In a controlled hydroponic comparison of red and green Salanoa butterhead lettuce grown under full-, half-, and quarter-strength macronutrient solutions, reducing nutrient solution strength produced significant shifts in the phenolic profile, with the largest changes observed in lignans and phenolic acids, followed by flavones and anthocyanins; fold-change values for specific phenolic subclasses ranged from approximately five-fold lower to eleven-fold higher relative to the full-strength control. The red cultivar showed a far stronger response than the green cultivar, with a significant genotype-by-nutrition interaction at p less than 0.001, demonstrating that pigmented genotypes are substantially more responsive to nutritional modulation than their non-pigmented counterparts even under identical treatment [23].

Potassium

Potassium plays a broadly enabling, rather than inhibitory, role in pigment accumulation. It is required for the carbon metabolism underpinning isoprenoid and flavonoid biosynthesis, contributes to phloem loading and assimilate transport, and is implicated in plant tolerance of multiple abiotic stresses that themselves often co-induce secondary metabolite accumulation [24]. Unlike nitrogen, potassium's relationship with pigmentation in the literature is generally supportive of supply rather than restriction, although quantitative, hydroponic-system-specific dose-response data meeting this review's verification standard were not identified and are flagged as a research gap in Section 8.

Phosphorus

Plant phosphate starvation signaling is governed by a well-characterized pathway in which PHR1, a MYB-family transcription factor, binds phosphate-starvation-responsive promoter elements and activates downstream phosphate starvation response genes, including the long-distance signaling microRNA miR399, which in turn suppresses the ubiquitin-conjugating enzyme PHO2 to enable systemic phosphate redistribution between shoot and root [25,26]. This pathway is one of the best-characterized nutrient-signaling cascades in plant biology. A direct mechanistic link between phosphate starvation and anthocyanin biosynthesis has been established in Arabidopsis: PHR1 binds directly to phosphate-starvation-responsive motifs, known as P1BS motifs, on the promoters of two anthocyanin pathway genes, flavanone 3'-hydroxylase, abbreviated F3'H, and leucoanthocyanidin dioxygenase, abbreviated LDOX, upregulating their transcription; loss-of-function phr1 mutants show significantly attenuated anthocyanin accumulation under phosphate-limiting conditions. Notably, PHR1 was shown to interact with the F3'H and LDOX promoters but not with DFR or PAP1, indicating a specific rather than pathway-wide regulatory action [3]. This is a genuine, verified molecular mechanism by which phosphate starvation drives anthocyanin accumulation, although it has been demonstrated in Arabidopsis rather than in a hydroponically grown crop species, and no quantified yield-versus-pigment trade-off data for timed phosphorus restriction in a commercial hydroponic crop meeting this review's sourcing standard could be identified. A specific quantitative claim present in an earlier draft of this review, describing a named blueberry phosphorus-timing study with a stated yield penalty, has been removed because the cited source does not exist. Translating the Arabidopsis PHR1 to F3'H and LDOX mechanism into a quantified, crop-specific hydroponic protocol is identified as a priority area for primary research in Section 8.

Magnesium and Sulphur

Magnesium is an obligate cofactor for chlorophyll biosynthesis via Mg-chelatase [21] and supports general plant metabolic capacity, including secondary metabolism, through its role as a cofactor for numerous enzymes. Sulphur contributes to pigment-pathway integrity indirectly through glutathione-mediated antioxidant protection of enzyme systems from reactive oxygen species damage, a well-established function of plant Sulphur metabolism [27]. Quantitative, hydroponic-specific dose-response studies isolating Sulphur's effect on pigment yield meeting this review's verification standard were not identified.

Micronutrient Effects on Pigment Enhancement

Iron speciation is a critical and frequently underappreciated determinant of pigment biosynthesis because several enzymes central to carotenoid and anthocyanin pathways are iron-dependent, including carotenoid desaturases and anthocyanidin synthase. Iron bioavailability in hydroponic nutrient solution is strongly pH-dependent: EDTA-chelated iron becomes substantially less plant-available above approximately pH 6.5 to 7.0, while EDDHA-chelated iron remains soluble and available across a wider pH range, a well-established principle of hydroponic iron management [28]. A specific quantitative claim regarding lycopene enhancement in hydroponic tomato through Fe-EDDHA substitution, present in an earlier draft of this review, could not be traced to a verifiable source and has been removed; the underlying chelation chemistry, however, is well supported by established literature and is retained as mechanism. Zinc is required for the structural integrity of C2H2 zinc-finger transcription factors and for numerous stress-responsive regulatory proteins; zinc deficiency is well documented to compromise micronutrient-dependent transcriptional regulation broadly, including in pathways connected to phenolic metabolism, although direct, verified hydroponic pigment dose-response data specific to zinc were not located within this review's verification scope [29]. Silicon, selenium, and manganese were addressed in an earlier draft of this review with specific percentage enhancements attached to named studies; none of those citations could be verified, and the associated claims have been removed pending location of a genuine source. Manganese's general physiological role as a cofactor for the photosystem II oxygen-evolving complex and for manganese superoxide dismutase is well established [27] and is retained here as background mechanism only, without an associated pigment-enhancement percentage.

Bio stimulants

The best-verified quantitative finding in this review comes from a controlled hydroponic floating-raft trial in which carrot and dill microgreens were treated with a legume-derived protein hydrolysate bio stimulant at 0.3 milliliters per liter of nutrient solution. In carrot, this treatment produced a 461.7 percent increase in total anthocyanin concentration and a 12.4 percent increase in total phenolic content relative to untreated controls. The response was strongly species-specific: dill microgreens under the same treatment did not show the same anthocyanin enhancement, instead showing increased fresh yield, up 13.5 percent, and increased ascorbic acid content, up 17.2 percent, demonstrating that bio stimulant-driven pigment enhancement is genotype- and species-gated rather than universal [1]. Mechanistically, protein hydrolysates are understood to act as signaling bio stimulants rather than simple nitrogen sources, with bioactive peptide fragments capable of triggering plant signaling cascades distinct from bulk nutrient effects [30,31]. The carrot and dill contrast

above is consistent with this signaling-based, genotype-dependent model, although the specific receptor-level mechanism in this system has not been confirmed and should not be over-specified. Other bio stimulant claims present in an earlier draft of this review, including a strawberry microbial co-inoculation and potassium synergy figure and a tomato protein-hydrolysate gene-expression fold-change figure, were attached to citations that, on verification, were either real papers describing unrelated work or could not be located at all. These claims have been removed rather than retained in hedged form.

Light-nutrient interactions

Light quality is perceived through distinct photoreceptor systems-phytochromes for red and far-red wavelengths, cryptochromes for blue and UV-A-which converge on shared downstream signaling, principally the COP1-HY5 module, to influence the expression of genes in the flavonoid and anthocyanin pathways [32]. The magnitude of this response is genotype-dependent and varies with light intensity, spectral composition, and interaction with nutrient status; specific red-to-blue ratio recommendations should therefore be treated as crop- and cultivar-specific rather than universal. Two specific quantitative light-by-nutrient or light-by-treatment interaction claims present in an earlier draft of this review, a blue-light-by-potassium synergy figure in red lettuce and a UV-B-by-nitrogen synergy figure in basil, were attached to citations that could not be verified; in the basil case, a real paper by a similarly named author group existed but described a different crop, light treatment, and metabolite class than claimed. Both figures have been removed. The general principle that supplemental blue or UV-B light increases phenolic and flavonoid accumulation in leafy crops is well represented in the broader horticultural lighting literature, but a specific, verified super additive interaction coefficient meeting this review's sourcing standard was not identified and is flagged as a research priority in Section 8.

Genotype as a Determinant of Response Magnitude

A recurring and well-supported theme across the verified evidence in this review is that genotype determines the ceiling on nutrient- or light-induced pigment enhancement more strongly than any single environmental variable. In the Salanoa lettuce trial discussed in Section 3.1, the pigmented red cultivar responded far more strongly to identical nutrient-strength treatments than the non-pigmented green cultivar [25]. In the carrot and dill microgreen trial discussed in Section 5, the same bio stimulant treatment produced a large anthocyanin increase in one species and no comparable increase in the other [1]. Comparable cultivar-dependent anthocyanin variation under shared environmental conditions has also been documented in lettuce in response to temperature, where three related Lollo Rosso-type cultivars showed materially different anthocyanin and chlorophyll b responses to identical temperature treatments, indicating that cultivar-level genetic background, not temperature alone, set the magnitude of pigment response [33]. The clearest demonstration of genotype, in this case engineered genotype, as an upper bound on pigment accumulation comes from transgenic, rather than nutritional, intervention: heterologous expression of the snapdragon transcription factors Delila and Rosea1 under a fruit-specific promoter in tomato produced fruit accumulating anthocyanins throughout the flesh and peel at concentrations comparable to those found in blackberries and blueberries, substantially exceeding levels achievable in tomato through prior metabolic engineering approaches, and increasing hydrophilic antioxidant capacity approximately threefold [4]. This result illustrates that the biosynthetic capacity of a genotype, not nutrient or light input alone, ultimately bounds achievable pigment yield; nutritional and light-based interventions operate within whatever ceiling the plant's regulatory genotype permits. A claimed quantitative correlation between MYB10 promoter strength and nitrogen-response magnitude in strawberry, present in an earlier draft of this review, could not be traced to any verifiable source and has been removed. The general principle that allelic variation at MYB-family loci governs genotype-dependent anthocyanin responsiveness is well supported by the broader literature on MBW complex regulation [16] and is retained as established mechanism without an attached numerical correlation (Table 1 & 2).

Table 1: Quantitative findings retained in this review, all independently verified against primary sources.

Pigment Class	Crop / System	Intervention	Verified Result	Reference
Anthocyanins, total phenolics	Carrot microgreens (floating raft)	Legume-derived protein hydrolysate, 0.3 mL/L nutrient solution	Anthocyanins +461.7%; total phenols +12.4% (carrot); no comparable anthocyanin increase in dill under identical treatment	El-Nakhel et al. [1]
Anthocyanins and other phenolic subclasses	Red vs. green Salanova lettuce (hydroponic)	Full-, half-, and quarter-strength macronutrient solution	Fold-changes of approximately -5 to +11 across phenolic subclasses; red cultivar showed significantly greater response than green (genotype x nutrition interaction, $p<0.001$)	Senizza et al. [2]
Anthocyanins (engineered)	Tomato (transgenic)	Heterologous expression of snapdragon Del/Ros1 transcription factors	Whole-fruit anthocyanin accumulation at concentrations comparable to blackberry/blueberry; approximately threefold increase in hydrophilic antioxidant capacity	Butelli et al. [4]
Anthocyanin, chlorophyll b	Lollo Rosso-type lettuce cultivars	Growth temperature (20C vs. 30C)	Cultivar-dependent differences in temperature response; growth at 30C reduced anthocyanin and chlorophyll b relative to 20C, with magnitude differing by cultivar	Gazula et al. [33]

Table 2: Verified transcription factors and regulatory mechanisms discussed in this review.

Factor / Mechanism	Pigment Class	Role	Trigger	Reference
MYB-bHLH-WD40 (MBW) complex	Anthocyanins	Master transcriptional activator complex	Convergence points for light and nutrient signals	Ramsay and Glover [16]
LBD37/38/39	Anthocyanins (repression)	Transcriptional repressors of anthocyanin pathway genes	Induced by nitrate; repress PAP1/MYB75 under N-replete conditions	Rubin et al. [23]
COP1-HY5	Light-regulated pigments generally	COP1 degrades HY5 in darkness; light inhibits COP1, allowing HY5 to activate light-responsive promoters	Phytochrome/cryptochrome activation by light	Lau and Deng [32]
PIF3/4/5	Carotenoids (suppression of PSY)	Suppress phytoene synthase in darkness; degraded under red light via phytochrome B	Light/dark transitions	Leivar and Quail [17]
CYP76AD (P450)	Betalains	Converts tyrosine to L-DOPA, the committed step toward betalamic acid	Constitutive in betalain-producing Caryophyllales	Hatlestad et al. [19]
PHR1	Anthocyanins (specific genes)	Binds P1BS motifs on F3'H and LDOX promoters (not DFR/PAP1); upregulates their transcription under Pi starvation	Phosphate deficiency	Liu et al. [3]
PHR1 / miR399-PHO2	Phosphate-responsive genes generally	Master regulator of Pi starvation response; activates miR399, which suppresses PHO2 for systemic Pi redistribution	Phosphate deficiency	Rubio et al. [25]; Pant et al. [26]

Research Gaps and Priorities

The verification process underlying this review removed a substantial majority of the specific quantitative claims present in earlier drafts, because the cited sources either did not exist, did not describe the claimed experiment, or were real papers whose content had been misrepresented. Rather than treat this as a setback, the resulting gaps are presented here as genuine, current priorities for primary research. First, whether deliberate, time-restricted phosphorus limitation can enhance anthocyanin accumulation without yield penalty in a hydroponic fruiting or leafy crop is mechanistically plausible given the PHR1 to F3'H and LDOX pathway, but has not, to this review's verification standard, been demonstrated and quantified for any hydroponic crop species. Second, super additive interactions between supplemental blue or UV-B light and macronutrient restriction are plausible given the shared convergence of light and nitrogen signaling, but a verified, quantified demonstration of such an interaction in a hydroponic crop was not located. Third, specific, hydroponic-system dose-response curves for silicon, selenium, and manganese against anthocyanin or carotenoid yield, with disease-resistance co-benefits, represent a genuine evidence gap. Fourth, given the strong and repeated genotype effects documented in Sections 3, 5, and 7, systematic genetic mapping of the loci responsible for differential nutrient- and light-responsiveness of pigmentation across cultivars would have high practical value for breeding programs targeting pigment-enhanced hydroponic crops. Fifth, cross-study comparison in this literature is hampered by inconsistent reporting of verified nutrient solution composition, pH, electrical conductivity, light spectrum and intensity, and pigment values on a consistent fresh- versus dry-weight basis; establishing minimum reporting standards would materially improve the reliability of future reviews in this area.

Conclusion

The mechanisms reviewed here, including nitrate-responsive LBD repression of anthocyanin genes, the COP1-HY5 light-signaling hub, PHR1-mediated phosphate-starvation signaling with its direct link to F3'H and LDOX transcription, iron chelation chemistry, and the central role of the MBW transcription factor complex, are well established in the plant molecular biology literature and provide a credible mechanistic basis for hydroponic pigment management. However, the verified evidence base for specific, quantified pigment enhancements achievable through hydroponic nutrient or light manipulation is considerably narrower than is often implied in review literature on this topic. Two findings stand out as genuinely robust: A large, genotype-specific anthocyanin increase in carrot microgreens following protein hydrolysate bio stimulant treatment [1], and a clear demonstration that pigmented genotypes respond far more strongly than non-pigmented genotypes to identical nutrient-strength treatments [2]. Genotype, more than any single nutritional or light variable, appears to set the practical ceiling on what hydroponic pigment management can achieve, a conclusion reinforced by engineering-scale evidence from transgenic tomato [4]. Realizing the broader promise of hydroponic systems for pigment and natural dye production will depend on primary research that closes the specific gaps identified in Section 8, conducted and reported to a standard that allows confident reuse by future reviewers. By establishing which nutrient- and light-based levers on pigment biosynthesis are genuinely supported by primary evidence, and which remain unverified despite frequent citation in the review literature, this synthesis provides a reliable mechanistic foundation for hydroponic systems to be developed as a resource-efficient, reproducible complement to field- and wild-sourced natural pigments-reducing pressure on land, water, and wild plant populations without overstating what current evidence supports.

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