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UDC 635.64:631.544:628.9 **Research article**

Beyond the yield: light spectrum as a driver of phenotypic reorganization in greenhouse tomato production

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Abstract

Background and Aim. Supplemental lighting is an essential factor influencing crop's productivity under greenhouse conditions. It plays a significant role not only in the yield enhancement but also for the biochemical and phenotypic reorganization of plants.

Materials and Methods. In this study, we evaluated the effect of LED lighting on the tomato plants grown under greenhouse conditions. A multivariate analysis approach was applied to assess how different light spectra reorganize tomato growth, yield, and biochemical quality.

Results. Distinct phenotypic strategies were observed. A red-dominant LED-spectrum demonstrated a stronger effect on fruit yield, increased leaf area, reduced fruit nitrate content, and enhanced nitrogen assimilation. In contrast, a balanced LED-spectrum increased fruit titratable acidity and pigment content.

Conclusion. A strong positive correlation was observed between canopy architecture, yield, pigment content, and nitrogen assimilation. The findings highlight the important role of supplemental lighting in goal-oriented tomato production under greenhouse conditions.

Keywords: LED supplemental lighting; spectral composition; tomato (Solanum lycopersicum L.); photosystem II efficiency; nitrate accumulation; phenotypic reprogramming.

Introduction

Supplemental lighting is an important factor influencing crop's productivity in the greenhouse conditions. The role of the supplemental lighting is important not only for the yield enhancement but also for the biochemical and phenotypic reorganization of plants [1, 2, 3]. In Northern Kazakhstan, daily light intensity often falls below 15 mol m^{-2} d^{-1}; thus supplementary lighting is necessary for sustainable crop production. In the past, high-pressure sodium (HPS) lamps were predominantly used due to their high radiant output and operational robustness [4, 5]. However, HPS systems are considered inefficient in large-scale production due to declining photon efficacy and substantial radiant heat output [6, 7]. The transition toward light-emitting diode (LED) technology has therefore been driven in the last decades [8, 9]. Plant responses to LED lighting are strongly dependent on spectral quality [10, 11]. In tomato, red and blue wavelengths regulate photomorphogenesis through phytochrome and cryptochrome-mediated pathways, affecting growth and photosynthetic capacity [12-16]. Recent studies demonstrate that intra-canopy and spectrally optimized LED systems can outperform conventional top-lighting approaches in enhancing yield and light-use efficiency [17, 18, 19].

Adjustments in chlorophyll antenna organization and the chlorophyll a/b ratio are strongly affected by the light spectral quality [20, 21]. In particular, light spectrum affects carotenoid content which

functions in plants as antioxidants and redox modulators, integrating photoprotection and metabolic signaling [22]. Spectral conditions can shift the balance between growth, yield and plant defense, affecting whole-plant metabolic allocation patterns [23, 24]. Additionally, light spectrum can serve as a regulator of nitrogen metabolism by affecting carbon availability, cytosolic redox status, and nitrate reductase activity [25, 26]. Recent studies demonstrate that red–blue spectral combinations reduce fruit nitrate concentration in hydroponically grown tomatoes [27-29]. However, whether commercially differentiated LED spectra simultaneously optimize productivity and nitrogen-use efficiency remains insufficiently explored [30, 31]. Additionally, few studies integrate a broad set of traits to understand the effect of spectral composition on general phenotypic strategies rather than focusing on individual trait responses [32-34]. The present study addresses these gaps by combining precise spectral characterization of two commercially relevant LED systems with comprehensive phenotypic profiling of greenhouse-grown tomatoes under Northern Kazakhstan conditions.

Materials and Methods

Plant Material and Cultivation Practices

The experiment was conducted during the winter–spring growing season (November 2024–March 2025) in a modern multi-span polycarbonate greenhouse located in Northern Kazakhstan (51°N) [35, 36]. Day/night air temperatures were maintained at 24 ± 2 °C and 18 ± 2 °C, respectively and relative humidity was maintained at 60–70%. Tomato (Solanum lycopersicum L.) plants of the indeterminate hybrid ‘Forticia F1’ were grown in a hydroponic system using mineral wool slabs (100×20×7.5 cm) according to standard commercial practices [37]. Seedlings were transplanted at the 3–4 true leaf stage (35 days after sowing). Plant density was 2.5 plants m^{-2}. Nutrition was supplied via drip irrigation using a modified Hoagland nutrient solution. Electrical conductivity (EC) was maintained between 2.5–3.0 dS m^{-1} depending on solar irradiance, and pH was maintained at 5.8 ± 0.2. All agronomic practices, including irrigation regime, pruning, and integrated pest management, were standardized across treatments to isolate the effects of spectral composition.

Lighting Treatments and Experimental Design

The experiment followed a randomized complete block design (RCBD) with three lighting treatments and five blocks per treatment (n = 15 biological replicates per treatment). Three supplemental lighting regimes were evaluated:

• HPS (Control): High-pressure sodium lamps (Son-T Agro, Philips), emitting a broad spectrum with a dominant yellow–orange region.

• KSDO1 (Balanced LED): Custom LED system (Led System Media, Kazakhstan) with a balanced blue:red ratio (peaks at 450 nm and 660 nm), including green and far-red components.

• KSDO2 (Productivity LED): Custom LED system with a red-dominant spectrum optimized for photon efficacy and biomass production (table 1).

Table 1. Spectral characteristics of supplemental lighting treatments used for greenhouse tomato cultivation

Lighting treatment	Spectral description	Main spectral peaks / regions	Blue–violet photon share, 380–499 nm (%)	Green photon share, 500–599 nm (%)	Red photon share, 600–699 nm (%)	Far-red photon share, 700–780 nm (%)	Red:blue photon ratio
HPS control	Broad yellow–orange spectrum with narrow emission peaks	~450 and ~590 nm	11.2	45.1	36.9	6.9	3.3

Continuation of Table 1

KSDO1	Broad balanced LED spectrum including blue, green, red, and far-red regions	Broad maximum at ~460–520 nm; extended red/far-red tail	25.6	28.6	26.5	19.2	1.0
KSDO2	Red-enriched LED spectrum with a distinct blue peak and broad red/orange region	~450 nm and ~600 nm	15.6	38.9	40.3	5.2	2.6

All lighting systems provided a canopy-level PPFD of 200 ± 10 μmol m^{-2} s^{-1}, measured using a quantum sensor (LI-190R, LI-COR Biosciences, USA). The photoperiod was 17 h (06:00–23:00), resulting in a supplemental DLI of approximately 12.2 mol m^{-2} d^{-1}. Light intensity and spectral distribution were verified using a calibrated spectroradiometer.

Phenotypic Measurements

Plant height, internode length, and stem diameter were measured biweekly. Stem diameter was recorded at a fixed internode using a digital caliper. Leaf area was determined destructively at flowering using a leaf area meter (LI-3100C, LI-COR Biosciences, USA) on three representative leaves per plant [20].

Maximum quantum yield of photosystem II (Fv/Fm) was measured on the third fully expanded leaf using a pulse-amplitude modulated fluorometer (Mini-PAM-II, Walz GmbH, Germany). Prior to measurement, l eaves were dark-adapted for 30 min to ensure full relaxation of reaction centers [38, 39].

Leaf samples were immediately frozen in liquid nitrogen and stored at −80°C. Chlorophyll a, chlorophyll b, and total carotenoids were extracted in 95% ethanol in the dark at 4 °C for 24 h. Absorbance was measured at 470, 649, and 665 nm using a UV–Vis spectrophotometer (Shimadzu UV-1800, Japan). Pigment concentrations were calculated according to *Lichtenthaler* and *Buschmann* (2001) [40] and *Wellburn* (1994) [41]. The chlorophyll a/b ratio was used as an indicator of light-harvesting antenna organization [19].

Harvesting was conducted twice weekly at the red-ripe stage. Total yield was calculated as cumulative fresh weight of marketable fruits per plant. For biochemical analyses, five representative fruits per replicate were homogenized to obtain composite samples.

• Nitrate concentration was determined using the salicylic acid colorimetric method [40], with absorbance measured at 410 nm [27, 28].

• Total soluble solids (TSS) were measured using a digital refractometer (Atago PAL-1, Japan) and expressed in °Brix.

• Titratable acidity (TA) was determined by titration with 0.1 N NaOH to pH 8.1 and expressed as % citric acid.

• Vitamin C content was quantified using the 2,6-dichlorophenolindophenol (DCPIP) titration method [41].

Statistical Analysis

Data normality and homogeneity of variance were assessed using Shapiro–Wilk and Levene's tests, respectively. Differences among treatments were evaluated by one-way ANOVA followed by Tukey's HSD test at $p \leq 0.05$. For trait integration, data were $\log10(\times + 1)$-transformed and Z-score standardized. Pearson correlation matrices, hierarchical clustering (Euclidean distance, Ward's linkage), and radar plots were generated in Python using Matplotlib and NumPy. This approach enabled the identification of coordinated phenotypic responses across lighting treatments.

Results

Effects of lighting regimes on plant canopy architecture

Both LED treatments (KSDO1 and KSDO2) increased assimilative surface area compared with the HPS control. Leaf area was increased by 7% under KSDO1 and 9% under KSDO2 ($p < 0.001$), with no significant difference between the two LED spectra. Internode length decreased by 5% in both KSDO1 and KSDO2 relative to HPS ($p < 0.01$), resulting in a more compact canopy structure. Stem diameter showed significant increase under both LED treatments ($p < 0.05$). Total fruit yield increased by 76.9 and 88.5% under KSDO1 and KSDO2, respectively, compared to control.

Interestingly, fruit quality traits responded differentially to spectral treatments. Titratable acidity and dry mass of fruit were significantly increased under KSDO1 as compared with the control ($p < 0.05$). A pronounced effect was observed for fruit nitrate concentration in KSDO2 with reduced nitrate levels by 26.7% as compared to control ($p < 0.001$) (Figure 1).

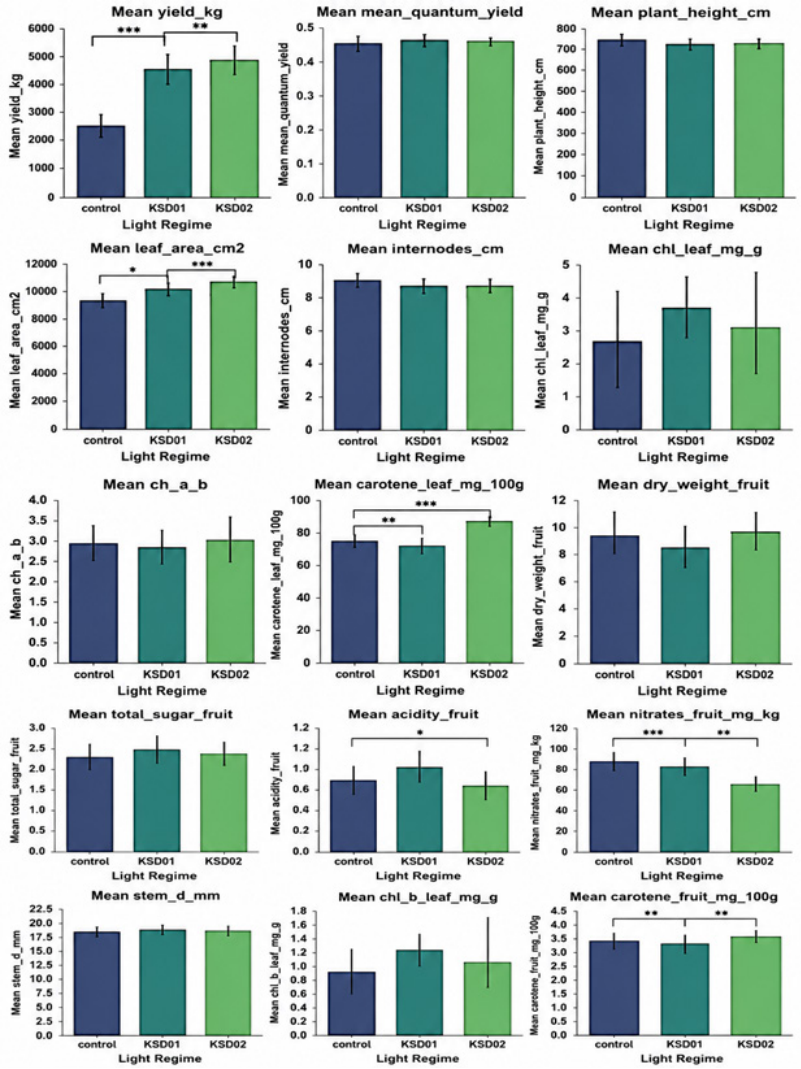

Figure 1. Effects of different lighting regimes on phenotypic parameters of greenhouse-grown tomato (*Solanum lycopersicum L.*), including total fruit yield, plant height, internode length, stem diameter, leaf area, maximum quantum yield of photosystem II (Fv/Fm), pigment composition, and fruit biochemical quality. HPS, high-pressure sodium lighting control; KSDO1, balanced LED spectrum; KSDO2, red-dominant productivity LED spectrum; LED, light-emitting diode; PSII, photosystem II; Fv/Fm, maximum quantum yield of photosystem II; chl a, chlorophyll a; chl b, chlorophyll b; chl a/b, chlorophyll a-to-b ratio; carotene, total carotenoids; SE, standard error. Data are presented as means ± SE (n = 15). Different lowercase letters indicate significant differences among treatments according to Tukey's HSD test at $p \leq 0.05$. Where asterisks are shown, *, **, and *** indicate significance at $p \leq 0.05$, $p \leq 0.01$, and $p \leq 0.001$, respectively

Integrated phenotypic patterns revealed by phenotypic profiling

The spider plot summarizes scaled average values of growth, photosynthetic, and fruit quality traits, providing an integrative comparison of phenotypic profiles induced by the three lighting regimes (Figure 2). The control treatment displays a generally reduced phenotypic envelope, with lower values for most growth- and yield-related traits, confirming its baseline status. In contrast, both LED treatments exhibit expanded profiles on fruit yield, leaf area and chlorophyll contents, indicating broad stimulation of plant performance. Along with this, KSDO2 demostrated the strongest enhancement of leaf carotenoids and fruit vitamin C, while KSDO1 displayed greater fruit sugar content and greater stem diameter forming the most pronounced peaks for these traits. Overall, the spider plot demonstrates that LED lighting does not induce a uniform enhancement of all traits but rather reorganizes the phenotypic balance of tomato plants.

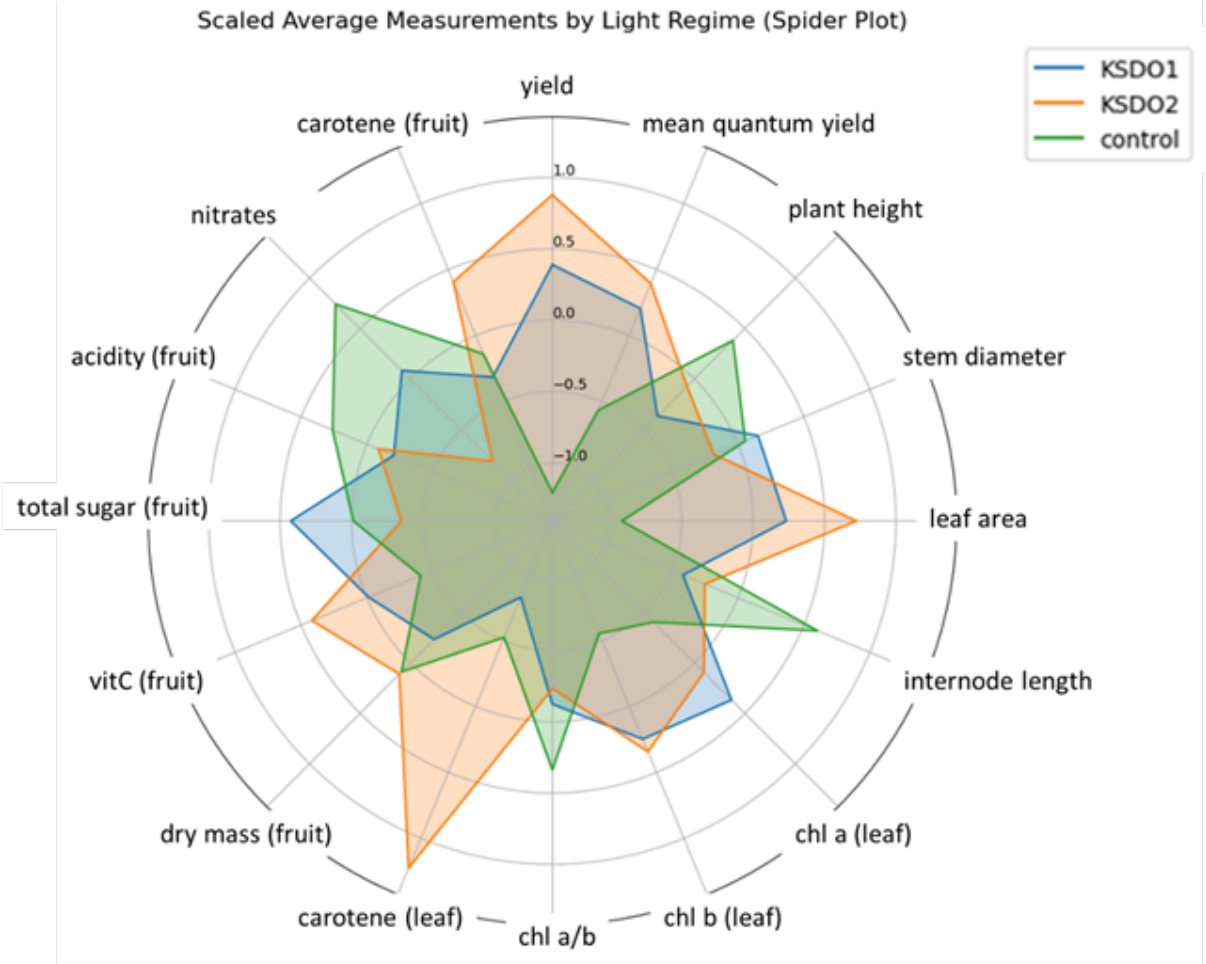

Figure 2. Spider/radar plot showing scaled mean values of log-transformed phenotypic traits for tomato plants grown under three lighting regimes. HPS, high-pressure sodium lighting control; KSDO1, balanced LED spectrum; KSDO2, red-dominant productivity LED spectrum; chl a, chlorophyll a; chl b, chlorophyll b; chl a/b, chlorophyll a-to-b ratio; carotene, total carotenoids; vit C, vitamin C content. Trait values were log10(× + 1)-transformed and Z-score standardized before plotting. Larger polygon areas indicate higher overall relative phenotypic expression across the measured traits

Correlation structure of growth, photosynthetic and fruit quality traits

The clustered heatmap reveals a highly structured correlation network among growth, photosynthetic, pigment, yield, and fruit quality traits, indicating coordinated physiological regulation rather than independent trait responses (Figure 3). Hierarchical clustering separates the traits into several well-defined functional groups. Yield is strongly positively correlated with leaf area ($r \approx 0.70$) and moderately

correlated with mean quantum yield, confirming that canopy development and photosynthetic performance jointly contribute to productivity. Leaf carotenoids show moderate positive correlations with yield and leaf area, but a strong negative correlation with fruit nitrate concentration ($r \approx -0.77$). Fruit carotenoids cluster separately from leaf carotenoids, displaying weaker correlations with growth traits but a stronger association with fruit biochemical parameters, indicating organ-specific regulation of secondary metabolism. Fruit nitrate concentration is negatively correlated with yield, leaf area, and mean quantum yield, highlighting a trade-off between nitrogen accumulation and productivity. In contrast, fruit acidity shows weaker correlations with growth traits and clusters closer to stem diameter and structural parameters, suggesting partial independence from primary growth processes.

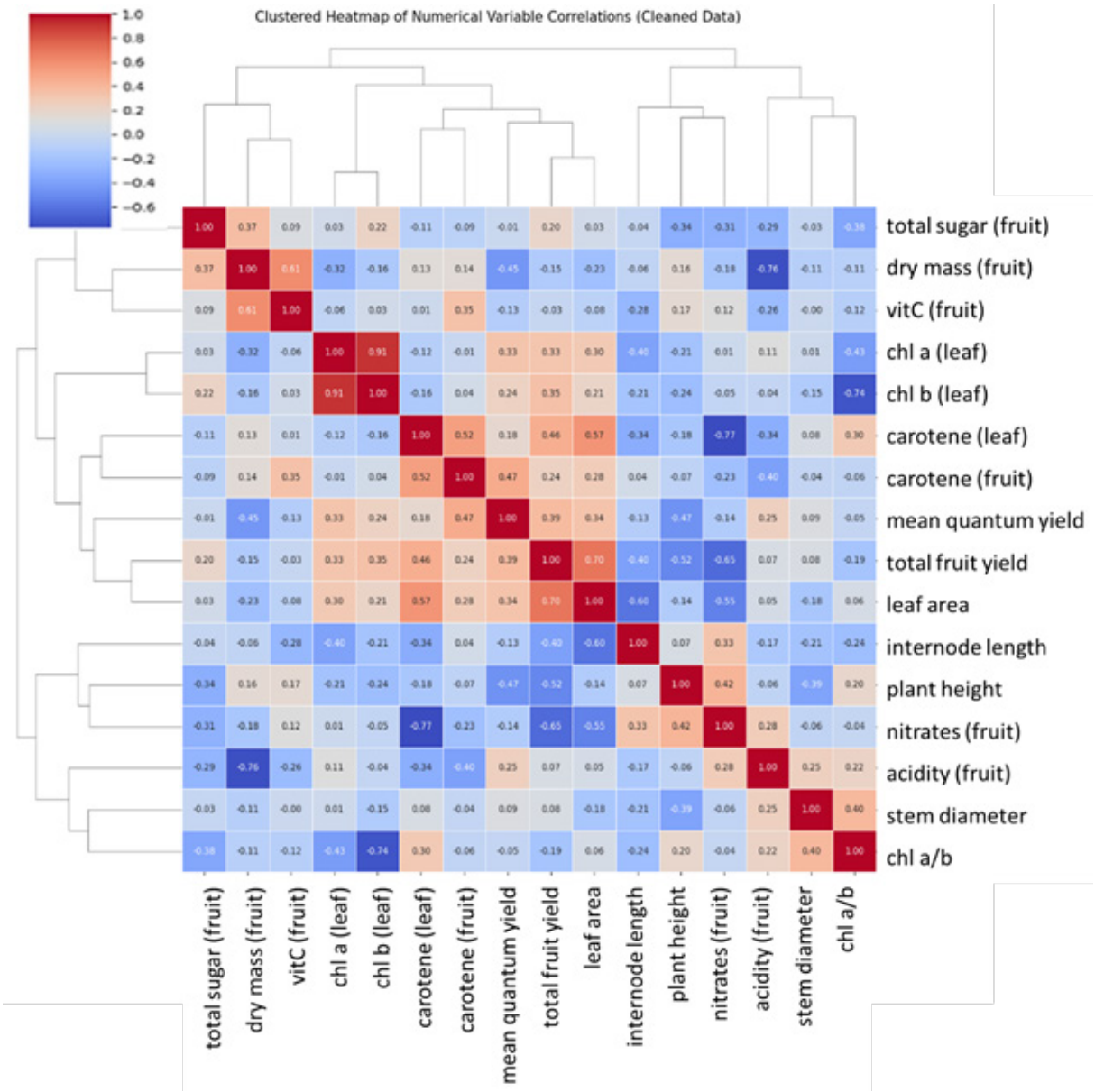

Figure 3. Pearson correlation matrix showing relationships among growth parameters, photosynthetic efficiency, pigment composition, yield, and fruit quality traits across all lighting treatments. Hierarchical clustering was performed using Euclidean distance and Ward's linkage. HPS, high-pressure sodium lighting control; KSDO1, balanced LED spectrum; KSDO2, red-dominant productivity LED spectrum; chl a, chlorophyll a; chl b, chlorophyll b; chl a/b, chlorophyll a-to-b ratio; carotene, total carotenoids; vitC, vitamin C content; nitrates, fruit nitrate concentration. Colors indicate Pearson correlation coefficients, with positive correlations shown in red and negative correlations shown in blue. Statistical significance is indicated as follows: *, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$, where applicable

Discussion

This study demonstrates that supplemental LED lighting reshapes the integrated phenotypic organization of greenhouse-grown tomato in a spectrum-dependent manner, even under identical photon flux density (PPFD). Light spectrum regulates plant architecture through the antagonistic interaction of phytochrome-and cryptochrome-mediated signaling pathways [14]. In this study, both LED treatments reduced internode length (~5%) and increased leaf area relative to HPS which is consistent with previous reports [12].

Pigment metabolism emerged as a primary target of spectral programming. Leaf carotenoid concentration increased significantly (16%) under the red-dominant KSDO2 regime. This response can be mechanistically explained by recent transcriptomic advances. Zhang et al. (2025) [41] recently identified that light quality regulates the tomato metabolome via SlDML2-mediated DNA demethylation. Specifically, the transcription factor SlHY5 (Elongated Hypocotyl 5), a central hub of light signaling, directly activates SlDML2, which in turn demethylates and upregulates genes involved in carotenoid biosynthesis. Our observation of divergent carotenoid accumulation between KSDO1 and KSDO2 parallels the findings of Ziaei et al. (2024) [17], who reported that specific LED spectra dramatically upregulated the Lycopene β-cyclase (LCY-B) gene. Our results suggest that under a balanced spectrum, resources were allocated more evenly between vegetative maintenance and secondary metabolism, whereas the yield-focused KSDO2 spectrum drove a metabolic shift toward accumulation, potentially mediated by epigenetic reprogramming as proposed in previous studies [23, 41].

A standout finding of this study is the 26.7% reduction in fruit nitrate concentration under KSDO2. Nitrogen assimilation is energetically costly and tightly coupled to photosynthetic electron transport. Guan et al. (2025) [27] recently elucidated the mechanism, showing that red light stimulates Nitrate Reductase (NR) activity more effectively than other wavelengths by modulating the cytosolic redox state (NADH availability) and inducing NR gene expression via phytochrome signaling. The red-dominant KSDO2 spectrum likely maximized the flow of electrons to ferredoxin and NADH, accelerating the reduction of nitrate (NO3-) to ammonium (NH4-) and its subsequent incorporation into amino acids. This explains the "low nitrate/high yield" phenotype. In contrast, the HPS control, with its lower photon efficacy in the red region, failed to drive NR activity to the same extent, leading to nitrate pooling in the vacuoles. This spectral regulation of nitrogen metabolism offers a practical tool for precision agriculture: growers can deploy red-rich spectra (like KSDO2) specifically to meet strict low-nitrate thresholds in fresh produce, a strategy supported by the broader findings of Ali et al. (2024) and Wang et al. (2022) [28, 29].

To summarize, our results demonstrate that different light spectra can be efficiently used for directed reprogramming of tomato growth, yield and fruit quality in greenhouse conditions. The results will be useful for commercial tomato production.

Authors' Contributions

AT: developed the concept, wrote the main part of the article, and supervised and approved the work; FK: collected and analyzed literature data and prepared the materials and methods sections; HD: explained the results and made scientific conclusions; RA: provided methodological support and carried out scientific editing work.

All authors read, reviewed, and approved the final version of the article.

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Өнімділіктен тыс: жылыжай қызанағын өндіруде фенотиптік қайта құрудың қозғаушы күші ретіндегі жарық спектрі

Турбекова А., Қожахметова Ф., Демир Х., Ақжүніс Р.

Түйін

Алғышарттар және мақсат. Қосымша жарықтандыру жылыжай жағдайында дақылдың өнімділігінде маңызды фактор болып табылады. Қосымша жарықтандырудың рөлі тек өнімділікті арттыру үшін ғана емес, сонымен қатар өсімдіктердің биохимиялық және фенотиптік қайта құрылуы үшін де маңызды.

Материалдар мен әдістер. Бұл зерттеуде біз жылыжай жағдайында өсірілген қызанақ өсімдіктеріне жарықдиодты жарықтандырудың әсерін бағаладық. Әртүрлі жарық спектрлерінің қызанақтың өсуін, өнімділігін және биохимиялық сапасын қалай қайта құратынын көру үшін көп айнымалы талдау әдісін қолдандық.

Нәтижелер. Әртүрлі фенотиптік стратегиялар анықталды: қызыл басым жарықдиодты спектр жеміс өнімділігіне, жапырақ ауданының ұлғаюына, жеміс нитратының азаюына және азоттың ассимиляциясының жоғарылауына күшті әсер етті. Керісінше, теңгерімді жарықдиодты спектр жемістің титрленетін қышқылдығы мен пигмент мөлшерін арттырды.

Қорытынды. Жапырақтың беткі құрылымы, өнімділік, пигмент мөлшері және азот ассимиляциясы арасында күшті оң корреляция байқалды. Қаржыландыру жылыжай жағдайында мақсатты қызанақ өндірісі үшін қосымша жарықтандырудың маңызды рөлін көрсетеді.

Кілт сөздер: жарықдиодты қосымша жарықтандыру; спектрлік құрамы; қызанақ (*Solanum lycopersicum L.*); фотожүйе II тиімділігі; нитраттың жиналуы; фенотиптік қайта бағдарламалау.

Помимо урожайности: световой спектр как фактор фенотипической реорганизации в тепличном производстве томатов

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Аннотация

Предпосылки и цель. Дополнительное освещение является важным фактором продуктивности культуры в тепличных условиях. Роль дополнительного освещения важна не только для повышения урожайности, но и для биохимической и фенотипической реорганизации растений.

Материалы и методы. В данном исследовании мы оценили влияние светодиодного освещения на растения томата, выращенные в тепличных условиях. Мы использовали многомерный анализ, чтобы увидеть, как различные спектры света влияют на рост, урожайность и биохимическое качество томата.

Результаты. Были выявлены различные фенотипические стратегии: светодиодный спектр с преобладанием красного цвета показал более сильное влияние на урожайность плодов, большую площадь листьев, снижение содержания нитратов в плодах и более высокую ассимиляцию азота. Напротив, сбалансированный светодиодный спектр увеличил титруемую кислотность плодов и содержание пигментов.

Заключение. Была обнаружена сильная положительная корреляция между архитектурой листового покрова, урожайностью, содержанием пигментов и ассимиляцией азота. Исследование подчёркивает важную роль дополнительного освещения для целенаправленного производства томатов в тепличных условиях.

Ключевые слова: дополнительное светодиодное освещение; спектральный состав; томат (*Solanum lycopersicum L.*); эффективность фотосистемы II; накопление нитратов; фенотипическое перепрограммирование.