



Article

Light Quality Regulates Source–Sink Dynamics and Mini-Tuber Formation in Aeroponic Potato

Zahra Mirzakhani ^{1,*}, Rahim Barzegar ^{1,*} , Sadeqh Mousavi-Fard ^{1,*} and Dimitrios Fanourakis ²

¹ Department of Horticultural Science, Faculty of Agriculture, Shahrekord University, Shahrekord 88186-34141, Iran; mandanaamirzakhani@gmail.com

² Laboratory of Quality and Safety of Agricultural Products, Landscape and Environment, Department of Agriculture, School of Agricultural Sciences, Hellenic Mediterranean University, Estavromenos, 71004 Heraklion, Greece; dfanourakis@hmu.gr

* Correspondence: barzegar@sku.ac.ir (R.B.); sadeghmosavifard@gmail.com (S.M.-F.)

Abstract

Light intensity and spectral composition regulate plant physiological processes and productivity, particularly under low-light greenhouse conditions. This study was designed to address two main objectives in aeroponically grown potato (*Solanum tuberosum* L. cv. Agria). First, we evaluated the effects of supplemental light quality, focusing on different red (R), blue (B), and white (W) combinations at a constant intensity of 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Second, we assessed the specific effects of far-red (FR) light on plant performance and biomass allocation patterns. Potato plants were grown under greenhouse conditions in a completely randomized design consisting of eight supplemental LED spectral treatments and a natural-light control. Supplemental lighting increased net photosynthesis, stomatal conductance, chlorophyll content, and biomass compared to the control, demonstrating that moderate increases in light intensity improved plant performance under low-light conditions. Among the spectral treatments, W light and balanced R–B combinations increased net photosynthetic rate by 93.7–198.7% and total biomass by 23.8–132.1% relative to the control, suggesting improved coordination of stomatal activity, electron transport, and chlorophyll biosynthesis under the experimental light environment. In contrast, FR inclusion reduced the net photosynthetic rate and mini-tuber biomass by 15.0–38.6% relative to the corresponding FR-free treatments, particularly under treatments with lower red proportions, suggesting that FR effects are more likely associated with phytochrome-mediated regulation of photosynthetic efficiency and assimilate partitioning under modified red to far-red spectral balance rather than classical shade-avoidance responses. Mini-tuber yield was strongly affected by light treatments. White light and balanced R:B spectra produced the highest tuber number and biomass, increasing mini-tuber number and biomass by 26.6–62.5% and 15.4–87.7%, respectively, compared with the control, whereas FR reduced yield. Although FR appeared to increase the relative allocation of biomass to tubers, overall photosynthetic performance and biomass accumulation remained lower, resulting in lower productivity. Overall, mini-tuber production appeared to be associated with source–sink relationships, where light intensity enhanced photosynthetic performance and biomass production, light quality optimized photosynthetic performance, and FR light appeared to modify biomass allocation patterns. These findings highlight the importance of optimizing spectral composition and FR management in aeroponic seed potato production under low-light greenhouse conditions.



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1. Introduction

Potato (*Solanum tuberosum* L.) is a major global crop, propagated vegetatively through seed tubers, a practice that promotes pathogen accumulation and yield decline over successive cycles. The production of disease-free planting material is therefore essential, with mini-tubers derived from in vitro plantlets representing the foundation of pre-basic seed systems [1]. Aeroponic cultivation has emerged as an efficient platform for mini-tuber production, as it enhances root oxygenation, nutrient delivery, and sanitary control [2]. However, the productivity of aeroponic systems is strongly governed by environmental regulation, particularly light, which controls both carbon assimilation and developmental signaling [3].

Light acts not only as the energy source for photosynthesis but also as a central regulator of plant physiological processes through photoreceptor-mediated signaling [4,5]. In the context of climate change, increasing variability in light conditions and radiation quality further emphasizes the importance of light-driven regulatory mechanisms, as plants must continuously adjust to dynamic and suboptimal environments [6]. Red (R) and blue (B) wavelengths are primarily absorbed by chlorophyll and drive photosynthetic electron transport, while also regulating stomatal conductance through phototropin activation and influencing chloroplast development via cryptochrome signaling [7]. In contrast, far-red (FR) light modifies the red-to-far-red ratio perceived by phytochromes, shifting the balance between active and inactive forms and thereby altering gene expression, biomass allocation patterns, and developmental programs [8]. These light-driven signaling networks integrate with metabolic pathways to determine the efficiency of carbon fixation and its subsequent distribution between source and sink organs [9]. Previous studies have demonstrated that light spectral composition strongly influences plant architecture, photosynthetic efficiency, assimilate partitioning, and storage organ development in controlled environment agriculture [10–12]. While balanced red and blue spectra are generally associated with enhanced photosynthetic performance and biomass accumulation, far-red light can modify photomorphogenic signaling related to growth regulation and physiological balance under modified spectral environments, source–sink relationships, and developmental signaling. However, these responses remain highly species- and environment-dependent, particularly under low-light greenhouse conditions where supplemental lighting contributes substantially to daily carbon gain.

In potato, tuber formation represents a strong sink-driven process that depends on both assimilate availability and hormonal regulation [13]. Light quality can influence tuberization indirectly by modulating photosynthetic performance and directly through phytochrome-mediated control of growth regulation and assimilate partitioning processes [14]. Although previous studies have shown that balanced red and blue spectra can enhance photosynthesis and biomass accumulation, and that far-red light influences developmental signaling and shade-avoidance responses, the extent to which these spectral effects regulate physiological coordination among photosynthesis, growth, and biomass partitioning in potato mini-tuber systems remains insufficiently resolved. In particular, limited information is available regarding how spectral composition simultaneously affects carbon assimilation, biomass allocation patterns, and mini-tuber formation under aeroponic low-light greenhouse conditions [3]. Recent studies have further highlighted the importance of LED spectral regulation in controlling morphophysiological traits, biomass

accumulation, nutritional quality, and stress responses under controlled environment cultivation. For example, recent work demonstrated that spectral composition can significantly influence photosynthetic performance, plant architecture, and product quality attributes under artificial lighting conditions, emphasizing the importance of optimizing light spectra according to crop-specific physiological responses and production objectives [15]. These findings reinforce the growing interest in precision spectral management as a strategy to improve both productivity and crop quality in controlled environment agriculture.

This limitation is particularly critical under low-light greenhouse environments, where reduced irradiance constrains photosynthesis and alters source–sink relationships [16]. Supplemental LED lighting provides an opportunity to manipulate spectral composition; however, the extent to which specific spectra regulate carbon assimilation versus biomass allocation patterns has not been clearly resolved in potato mini-tuber systems [17]. Because the natural-light control differed from LED treatments in both light intensity and spectral composition, comparisons with the control primarily reflect the effects of supplemental lighting under low natural irradiance, whereas comparisons among LED treatments isolate spectral effects.

Therefore, the objectives of this study were twofold. First, to evaluate the effects of supplemental light quality, focusing on different red (R), blue (B), and white (W) combinations applied at a constant intensity, on physiological performance, growth, and mini-tuber production. Second, to assess the specific role of far-red (FR) light in modulating carbon assimilation and biomass allocation patterns in aeroponic potato. Emphasis was placed on identifying light-driven mechanisms linking photosynthetic performance with biomass distribution responses, providing a physiological framework for optimizing light management in controlled environment seed potato production. In the present study, source–sink relationships were evaluated indirectly through integrative physiological, biomass allocation, and productivity-related responses rather than through direct quantification of carbohydrate transport or assimilate fluxes. We hypothesized that: (i) balanced red–blue and white light spectra would enhance photosynthetic performance and mini-tuber productivity by improving stomatal regulation, photochemical efficiency, and carbon assimilation; and (ii) far-red light inclusion would alter source–sink relationships through phytochrome-mediated signaling, promoting biomass allocation toward elongation growth at the expense of biomass accumulation and mini-tuber yield.

2. Materials and Methods

2.1. Experimental Design, Plant Material, and Aeroponic System

The experiment was conducted in a research greenhouse at Shahrekord University (Shahrekord, Iran; 32°20' N, 50°51' E; 2070 m a.s.l.) using a completely randomized design with nine treatments and three replications. Treatments consisted of eight supplemental LED light spectra and a natural light control (Table 1). Spectral treatments included combinations of red (R), blue (B), white (W), and far-red (FR) light. The spectral distributions of the light sources are presented in Figure 1, while their key spectral characteristics, including peak wavelengths and emission ranges, are summarized in Table 2. White light (W) exhibited a broad spectral distribution across the photosynthetically active radiation range (400–700 nm) and was therefore not characterized by a single peak wavelength (Figure 1). To evaluate the role of FR, 10% of the total photon flux was allocated to FR in designated treatments, resulting in two groups: without FR and with FR (+FR). Thus, while total supplemental photon flux was maintained constant, FR inclusion reduced the proportion of PAR within the spectral distribution. Consequently, FR-containing treatments received approximately $90 \mu\text{mol m}^{-2} \text{s}^{-1}$ within the 400–700 nm PAR range and $10 \mu\text{mol m}^{-2} \text{s}^{-1}$

in the FR range, whereas non-FR treatments received $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ entirely within the PAR range, without inclusion of far-red radiation.

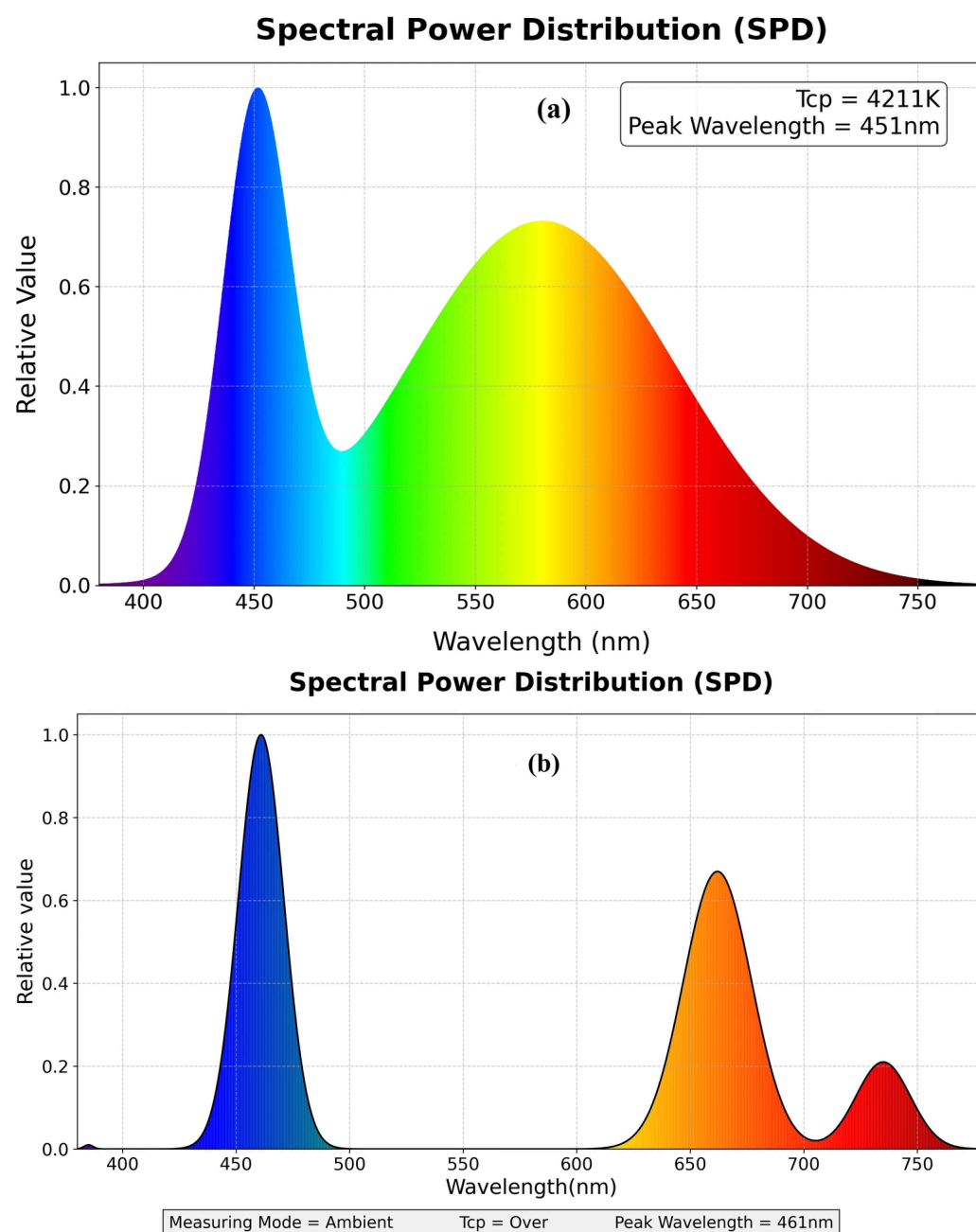


Figure 1. Spectral distribution of the white LED light source (a) and the red (R), blue (B), and far-red (FR) LED light sources (b) used in the supplemental lighting treatments applied in the greenhouse study.

LED fixtures were positioned 30 cm above the canopy and regularly adjusted to maintain a constant distance from the apical meristem. Supplemental LED treatments were applied at a constant intensity of $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ across all spectral combinations, allowing the effects of spectral quality and FR inclusion to be evaluated under a constant supplemental light intensity. Supplemental light operated from sunrise to sunset (approximately 08:00–17:00 h) throughout the experimental period from December to March, a period characterized by low natural irradiance and reduced daylength, in order to partially compensate for sub-optimal daily light integral (DLI) conditions for potato growth (Figure 2). Natural light intensity during the experimental period ranged between 76 and $413 \mu\text{mol m}^{-2} \text{s}^{-1}$ (mean approximately $220 \pm 90 \mu\text{mol m}^{-2} \text{s}^{-1}$; Figure 2). Based on the applied inten-

sity and photoperiod, supplemental lighting contributed approximately $3.6 \text{ mol m}^{-2} \text{ d}^{-1}$, representing about 25–35% of the total DLI during the experimental period.

Table 1. Supplemental LED spectral treatments applied to potato plants grown in an aeroponic system.

Treatment	Spectral Components	Spectral Composition (%)	Abbreviation
1	Red (R)	100R	100R
2	Red (R)+Far-red (FR)	90R+10FR	90R+10FR
3	Red (R)+Blue (B)	75R:25B	75R:25B
4	Red (R)+Blue (B)+Far-red (FR)	67R:23B+10FR	67R:23B+10FR
5	Red (R)+Blue (B)	50R:50B	50R:50B
6	Red (R)+Blue (B)+Far-red (FR)	45R:45B+10FR	45R:45B+10FR
7	White (W)	100W	100W
8	White (W)+Far-red (FR)	90W+10FR	90W+10FR
9	Natural light	–	Control

Table 2. Spectral characteristics of LED light sources used in the experiment.

Spectrum	Peak Wavelength (nm)	Spectral Range (nm)
Blue (B)	~450	430–480
Red (R)	~660	640–680
Far-red (FR)	~730	710–750

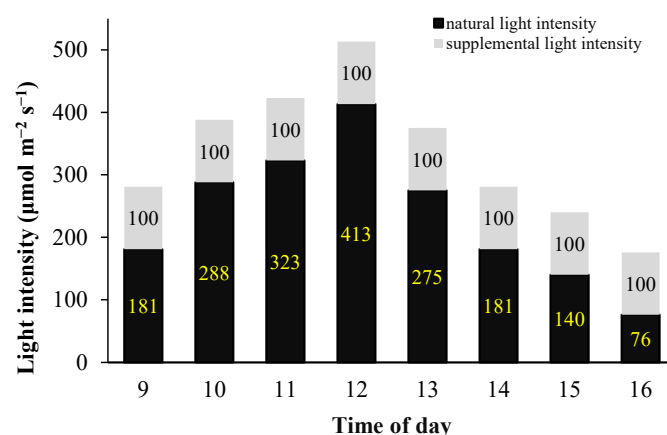


Figure 2. Diurnal variation in natural light intensity on a representative sunny day in December and the constant supplemental LED light intensity ($100 \mu\text{mol m}^{-2} \text{ s}^{-1}$) applied during the experiment.

Virus-free in vitro plantlets of potato (*S. tuberosum* L. cv. Agria), a widely cultivated and high-yielding cultivar commonly used in seed potato production systems due to its stable growth performance and strong tuberization capacity, were obtained from the Agricultural and Natural Resources Research Center of Ardabil (Khorramabad, Iran; $33^{\circ}29' \text{ N}$, $48^{\circ}21' \text{ E}$; 1147 m a.s.l.). After acclimatization, plantlets were transferred to a semi-closed aeroponic system. The aeroponic system was selected due to its ability to enhance root oxygenation, improve nutrient use efficiency, and promote uniform and enhanced mini-tuber production compared to substrate-based systems. A schematic representation of the aeroponic system and experimental setup is provided in Supplementary Figure S1.

The aeroponic units measured 1.2 m in height, 1 m in width, and 9 m in length, and the root zone was maintained in darkness using opaque covers to prevent light-induced inhibition of tuber formation. Plants were spaced at $20 \times 25 \text{ cm}$, corresponding to a density of 20 plants m^{-2} , a density selected to optimize canopy light interception while minimizing canopy shading and inter-plant competition, while ensuring adequate airflow and disease control under aeroponic conditions.

Greenhouse environmental conditions were maintained at 23 ± 2 °C during the day, 17 ± 1 °C at night, and 50–70% relative air humidity. A misting system delivered nutrient solution every 5 min for 15 s throughout the light period (08:00–17:00 h), using 30 µm nozzles. This intermittent misting regime ensured continuous root hydration and oxygen availability without inducing hypoxic conditions.

The nutrient solution had an electrical conductivity of 1.2 dS m^{-1} and pH 5.8 and contained (mg L^{-1}): 120 nitrogen (N), 31 phosphorus (P), 210 potassium (K), 120 calcium (Ca), 24 magnesium (Mg), 48 sulfur (S), 1.8 iron (Fe), 0.5 manganese (Mn), 0.3 zinc (Zn), 0.2 boron (B), 0.1 copper (Cu), and 0.05 molybdenum (Mo). The nutrient solution was prepared using analytical-grade fertilizers (e.g., $\text{Ca}(\text{NO}_3)_2$, KNO_3 , KH_2PO_4 , MgSO_4) and micronutrient salts. These concentrations were selected to provide a balanced nutrient supply tailored to potato growth under aeroponic conditions, supporting both vegetative development and tuber formation while minimizing the risk of nutrient limitations or toxicities.

The solution was monitored daily, replaced weekly, and the returned nutrient solution was disinfected using ultraviolet (UV) radiation (peak wavelength approximately 254 nm) to prevent microbial contamination and maintain system hygiene.

2.2. Chlorophyll Fluorescence Measurements

Chlorophyll fluorescence was measured to evaluate the photochemical efficiency and functional status of photosystem II (PSII). Measurements were performed on fully expanded, healthy leaves located at the upper canopy (3rd leaf from the apex) of three plants per replicate, consistent with gas exchange measurements. Specifically, measurements were taken on the terminal leaflet of the selected compound leaf, at the central lamina region midway between the midrib and the leaf margin, avoiding major veins to ensure consistent optical properties and reliable fluorescence measurements. Prior to measurement, leaves were dark-adapted for 30 min using light-exclusion clips to ensure complete oxidation of PSII reaction centers.

Fluorescence measurements were conducted using a portable pulse-amplitude modulated (PAM) fluorometer (Mini-PAM-II, Walz, Germany) under controlled conditions. Minimum fluorescence (F_0) was recorded under weak modulated light, followed by application of a saturating light pulse of $3000 \text{ µmol photons m}^{-2} \text{ s}^{-1}$ for 1 s to determine maximum fluorescence (F_m). No actinic light was applied during dark-adapted measurements. Variable fluorescence (F_v) was calculated as $F_m - F_0$, and the maximum quantum efficiency of PSII photochemistry was expressed as F_v/F_m . In addition, the performance index on an absorption basis (PI_{abs}), an integrative parameter reflecting energy conservation from photon absorption to electron transport processes, was calculated according to the standard JIP-test protocol.

Measurements were performed four days prior to destructive growth analysis on the same plants. All measurements were conducted during the morning period (09:00–11:00 h) to minimize diurnal variation and ensure comparability among treatments [18]. For each treatment, three biological replicates were assessed, with three plants per replicate and one leaf measured per plant. Plant-level measurements within each replicate were treated as subsamples and averaged prior to statistical analysis. Therefore, the replicate unit, rather than the individual plant, was considered the true experimental unit ($n = 3$).

2.3. Gas Exchange Measurements

Net photosynthetic rate (P_n) and transpiration rate (Tr) were measured using a portable photosynthesis system (CI-340, CID Bio-Science, Camas, USA). Measurements were performed on fully expanded, healthy leaves located at the upper canopy (3rd leaf from the apex) of three plants per replicate to ensure uniform physiological status.

Measurements were carried out under ambient greenhouse conditions. However, care was taken to ensure that measured leaves remained fully exposed to their respective light treatments during measurement. The leaf chamber conditions were allowed to stabilize prior to recording, and steady-state values were logged after approximately 60–90 s. The photosynthetic photon flux density (PPFD) incident on the measured leaf corresponded to the treatment-specific light environment (natural plus supplemental light), while air temperature (23 ± 0.1 °C), relative air humidity ($60 \pm 1\%$), and CO₂ concentration (380 ± 15 µmol mol^{−1}) remained close to ambient greenhouse conditions. Therefore, gas exchange measurements reflected both intrinsic physiological responses and the instantaneous treatment-specific light conditions during measurement, rather than intrinsic photosynthetic capacity under fully standardized chamber conditions. The system was calibrated prior to measurements according to the manufacturer's instructions.

Gas exchange measurements were conducted during the morning period (09:00–11:00 h) to minimize diurnal variation and avoid midday stomatal limitations. Measurements were performed on representative clear-sky days characterized by relatively stable greenhouse environmental conditions in order to minimize short-term fluctuations in irradiance and environmental variability among treatments. In addition, the order of treatment measurements was varied among measurement days to minimize potential temporal bias. Three gas exchange apparatuses were operated simultaneously, allowing measurements across treatments to be completed within a narrow temporal window and ensuring comparable physiological assessment among light treatments. The measurements were intended primarily to provide comparative physiological responses among treatments rather than estimates of integrated daily carbon assimilation. Measurements were performed four days prior to destructive growth analysis on the same plants used for chlorophyll fluorescence assessment. The same leaf area previously marked for fluorescence measurements was used to ensure direct comparability between physiological parameters.

For each leaf, multiple readings were taken and averaged to obtain a representative value. Data were expressed on a leaf area basis (µmol CO₂ m^{−2} s^{−1} for Pn and mmol H₂O m^{−2} s^{−1} for Tr). For each treatment, three biological replicates were assessed, with three plants per replicate and one leaf measured per plant. Plant-level measurements within each replicate were treated as subsamples and averaged prior to statistical analysis. Therefore, the replicate unit, rather than the individual plant, was considered the true experimental unit ($n = 3$).

2.4. Chlorophyll Content Determination

Chlorophyll a (Chl a), chlorophyll b (Chl b), and total chlorophyll (Chl) contents were determined spectrophotometrically following solvent extraction. Measurements were performed one day prior to destructive growth analysis, during the morning period (09:00–11:00 h), to ensure consistency with gas exchange and chlorophyll fluorescence measurements and to minimize diurnal variation.

Leaf samples were collected from fully expanded, healthy leaves located at the upper canopy (3rd leaf from the apex) of three plants per replicate. Specifically, disks were excised from the terminal leaflet at the central lamina region, midway between the midrib and the leaf margin, avoiding major veins to ensure uniform pigment extraction. Samples were immediately processed to minimize pigment degradation.

Chlorophyll pigments were extracted in 80% (*v/v*) acetone, followed by centrifugation to remove debris. Absorbance of the supernatant was measured at 663 nm and 647 nm using a UV–Vis spectrophotometer (PerkinElmer Lambda 25, Waltham, USA). Chlorophyll concentrations were calculated according to the equations of Lichtenthaler [19]:

$$\text{Chl a} = 12.25 \times A_{663} - 2.79 \times A_{647}$$

$$\text{Chl b} = 21.50 \times A_{647} - 5.10 \times A_{663}$$

$$\text{Total Chl} = 7.15 \times A_{663} + 18.71 \times A_{647}$$

Chlorophyll content was expressed on a fresh weight basis (mg g^{-1} FW). For each treatment, three biological replicates were assessed, with three plants per replicate and one leaf measured per plant. Plant-level measurements within each replicate were treated as subsamples and averaged prior to statistical analysis. Therefore, the replicate unit, rather than the individual plant, was considered the true experimental unit ($n = 3$).

2.5. Phenolic Compounds Analysis

Total phenolic compounds were determined using high-performance liquid chromatography (HPLC). Measurements were performed one day prior to destructive growth analysis, during the morning period (09:00–11:00 h), to ensure consistency with gas exchange, chlorophyll fluorescence, and chlorophyll content measurements and to minimize diurnal variation.

Leaf samples were collected from fully expanded, healthy leaves located at the upper canopy (3rd leaf from the apex) of three plants per replicate. Specifically, tissue was excised from the terminal leaflet at the central lamina region, midway between the midrib and the leaf margin, avoiding major veins to ensure uniform sampling. Samples were immediately processed to minimize oxidation and phenolic degradation.

Phenolic compounds were extracted using 80% (v/v) methanol, followed by centrifugation and membrane filtration (0.45 μm) prior to analysis. The extracts were analyzed using an HPLC system (Shimadzu Nexera series, Kyoto, Japan) equipped with a C18 reverse-phase column [20]. Separation was achieved using a gradient elution with solvent A (water with 0.1% formic acid) and solvent B (acetonitrile with 0.1% formic acid), starting at 5% B, increasing to 40% B over 30 min, then to 90% B at 35 min, followed by re-equilibration to initial conditions. The flow rate was set at 1.0 mL min^{-1} , and the column temperature was maintained at 30°C .

Detection was performed using a UV detector at 280 nm and 320 nm to target different classes of phenolic compounds. Individual phenolic compounds, including rutin, chlorogenic acid, caffeic acid, gallic acid, coumaric acid, tannic acid, and related derivatives, were identified and quantified based on retention times and calibration curves of authentic standards. Total phenolic content was calculated as the sum of the identified compounds and expressed on a fresh weight basis ($\mu\text{g g}^{-1}$ FW). For each treatment, three biological replicates were assessed, with three plants measured within each replicate as subsamples and averaged prior to statistical analysis. Therefore, the replicate unit, rather than the individual plant, was considered the true experimental unit ($n = 3$).

2.6. Growth and Mini-Tuber Yield Measurements

Growth and yield parameters were assessed to evaluate plant development and productivity under different light treatments. Growth parameters were measured at an intermediate developmental stage when vegetative development had stabilized, whereas yield parameters were assessed at full maturity to capture complete tuberization dynamics. Growth measurements were performed 80 days after transplanting, while mini-tuber yield was monitored throughout the experimental period and finalized at harvest (120 days after transplanting). The different timing reflects the fact that vegetative growth parameters reach a relatively stable stage earlier in the crop cycle, whereas mini-tuber formation and bulking are dynamic processes that continue until the end of the cultivation period.

Growth parameters included plant height, stem diameter, leaf number, total leaf area, and shoot fresh and dry weight. Plant height was measured from the base to the apical

meristem, and stem diameter was determined at the midpoint of the main stem using a digital caliper. Leaf number was recorded by counting fully expanded leaves. Leaf area was measured using image analysis [21]. Shoot fresh weight was recorded immediately after harvest, and dry weight was determined after oven-drying samples at 60 °C until constant weight.

Mini-tuber formation was first observed 55 days after transplanting. Tubers within the size range of 20–25 mm were harvested daily to avoid overgrowth and to standardize yield assessment, as this size class corresponds to commercially relevant pre-basic seed tubers and allows consistent comparison of tuber number across treatments. At the end of the experimental period (120 days after transplanting), all remaining tubers were harvested regardless of size.

Yield parameters included the total number of mini-tubers per plant, as well as the fresh and dry weight of mini-tubers. Mini-tuber dry weight was determined after slicing and oven-drying at 60 °C until constant weight. Biomass allocation was expressed as the percentage contribution of shoot and mini-tuber biomass to total plant biomass. All measurements followed a hierarchical sampling structure in which three biological replicates were used per treatment, with three plants per replicate treated as subsamples and averaged prior to statistical analysis; thus, the replicate was considered the experimental unit ($n = 3$).

2.7. Statistical Analysis

All data were analyzed using one-way analysis of variance (ANOVA) based on a completely randomized design (CRD). Although the experimental treatments included combinations of basal spectral composition and far-red (FR) inclusion, the experimental structure did not constitute a fully orthogonal factorial design due to the inclusion of a non-LED natural-light control and the absence of a FR-equivalent control treatment. Therefore, one-way ANOVA was used for the primary analysis of the complete dataset. However, because the LED treatments alone formed a balanced factorial structure, a supplementary two-way ANOVA was conducted on the LED subset, based on spectral base $\times$ far-red (FR) inclusion.

For each treatment, three independent biological replicates were used for statistical analysis. Within each replicate, three plants were evaluated as subsamples, and their values were averaged prior to ANOVA. Thus, the replicate was considered the experimental unit, with individual plants treated as subsamples to avoid pseudoreplication. Prior to analysis, all datasets were tested for normality and homogeneity of variances using the Shapiro–Wilk and Levene’s tests, respectively. When necessary, data were log- or square-root-transformed to satisfy ANOVA assumptions.

When significant treatment effects were detected, means were separated using Tukey’s honestly significant difference (HSD) test at $p \leq 0.05$. Results are presented as mean values $\pm$ standard error (SE) of three biological replicates ($n = 3$). All primary and supplementary statistical analyses were performed using Minitab software (Minitab V21 Inc., USA). Graphs were generated using Microsoft Excel and subsequently formatted for publication-quality presentation.

To complement the primary statistical analysis and provide targeted validation of key physiological and productivity-related responses, supplementary analyses were performed on five representative response variables: net photosynthetic rate (P_n), performance index on absorption basis (PI_{abs}), total plant biomass, mini-tuber biomass, and plant height. These variables were selected because they represent the major functional domains of plant response, including photosynthetic performance, photochemical efficiency, vegetative growth, and yield formation, thereby providing an integrative assessment of

light-driven physiological regulation. Two-way ANOVA (4×2) was applied to LED-only treatments to evaluate the effects of spectral base, far-red (FR) inclusion, and their interaction (Supplementary Table S1), while Dunnett's test was used to compare each LED treatment against the natural-light control (Supplementary Table S2). In addition, independent samples *t*-tests were conducted to assess differences between FR-containing and FR-free treatments within each spectral base (Supplementary Table S3).

The analytical framework was predefined to reflect the hierarchical experimental structure, with primary inference based on the completely randomized design (CRD) and confirmatory factorial decomposition applied to LED treatments to disentangle spectral base and far-red effects.

3. Results

3.1. Chlorophyll Fluorescence Parameters

Chlorophyll fluorescence parameters were only partially affected by the different supplemental LED light treatments (Figure 3). Minimum fluorescence (F_0) showed only minor treatment-related variation, whereas maximum fluorescence (F_m) did not differ significantly among treatments, indicating that the basal and maximal fluorescence yields of PSII remained stable across spectral conditions (Figure 3a,b).

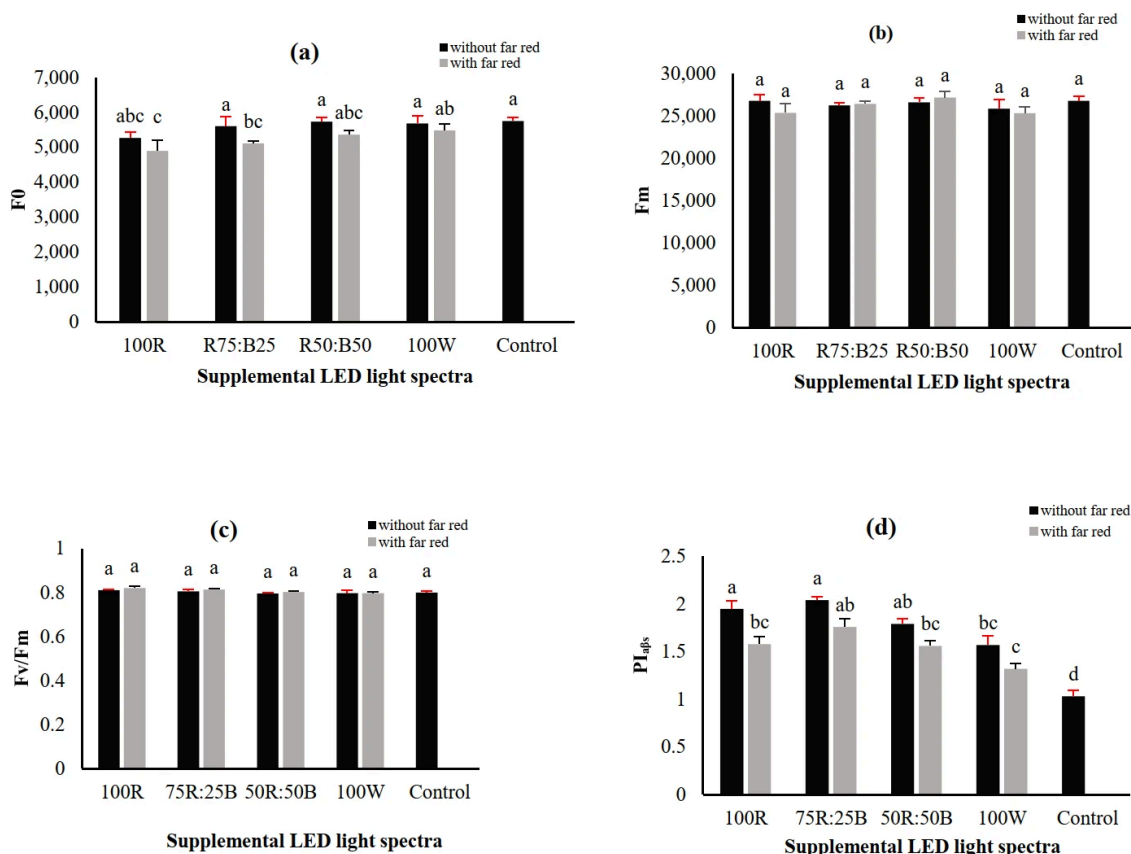


Figure 3. Effects of supplemental LED light spectra (spectral characteristics in Figure 1 and treatment composition in Table 1) on chlorophyll fluorescence parameters of potato (*S. tuberosum* L. cv. Agria): (a) minimum fluorescence (F_0), (b) maximum fluorescence (F_m), (c) maximum quantum efficiency of PSII (F_v/F_m), and (d) performance index on absorption basis (PI_{abs}). Values represent means $\pm$ SE ($n = 3$ biological replicates). Different letters indicate significant differences among treatments according to Tukey's honestly significant difference (HSD) test at $p \leq 0.05$. 100R, monochromatic red; 90R+10FR, red with 10% far-red; 75R:25B, red:blue (75:25); 67R:23B+10FR, red:blue (67:23) with 10% far-red; 50R:50B, red:blue (50:50); 45R:45B+10FR, red:blue (45:45) with 10% far-red; 100W, white; 90W+10FR, white with 10% far-red; Control, natural light.

Similarly, the maximum quantum efficiency of PSII photochemistry (F_v/F_m) showed no significant differences among treatments and remained within the optimal range for non-stressed plants, suggesting that PSII reaction centers were not adversely affected by the applied light spectra (Figure 3c).

In contrast, the performance index on an absorption basis ($PI_{a\beta s}$) was significantly influenced by light treatments (Figure 3d). $PI_{a\beta s}$ increased by 14.7–23.4% under white and balanced red–blue treatments compared with FR-containing treatments, indicating enhanced overall energy conservation efficiency. Treatments without far-red light exhibited higher $PI_{a\beta s}$ values compared to their corresponding far-red treatments, while balanced red–blue and white light treatments exhibited the highest values. Variations in $PI_{a\beta s}$ among treatments indicate differences in the overall efficiency of energy conservation from photon absorption to electron transport, suggesting differences in the functional performance of PSII beyond primary photochemical efficiency. These differences reflect up to 1.2% variation in PSII energy-use efficiency among treatments, highlighting changes in downstream electron transport performance. Although most fluorescence parameters were stable, $PI_{a\beta s}$ was up to 23.4% higher under non-FR treatments, indicating improved overall photosynthetic performance under optimized spectra.

Overall, while PSII efficiency (F_v/F_m) remained unchanged (<2% variation), spectral composition altered $PI_{a\beta s}$ by up to 23.4%, indicating effects on integrated photosynthetic performance rather than primary photochemistry.

Supplementary two-way ANOVA (4×2) on LED-only treatments confirmed significant main effects of spectral base and far-red (FR) inclusion on $PI_{a\beta s}$, as well as a significant interaction between the two factors (Supplementary Table S1). In addition, *t*-tests confirmed higher $PI_{a\beta s}$ values in FR-free treatments compared with their corresponding FR-containing counterparts across spectral bases (Supplementary Table S3).

3.2. Gas Exchange Responses to Light Quality

Supplemental LED light spectra significantly affected gas exchange parameters of potato plants (Figure 4). Net photosynthetic rate (P_n) varied markedly among treatments (Figure 4a). The highest P_n values were observed under white light (100W) and balanced red–blue combinations (75R:25B and 50R:50B), indicating enhanced photosynthetic performance under broad or mixed spectra. In contrast, the inclusion of far-red light (FR) was associated with lower P_n across all spectral combinations, as evidenced by lower values in 90R+10FR, 67R:23B+10FR, 45R:45B+10FR, and 90W+10FR compared to their respective FR-free counterparts. Monochromatic red light (100R) resulted in intermediate P_n values, lower than balanced R:B and white light treatments but higher than FR-containing treatments. Importantly, P_n increased by 93.8–198.7% under white and balanced red–blue treatments compared with the control, further confirming enhanced carbon assimilation under optimized spectra. FR-containing treatments reduced P_n by 1.1–94.9% compared with FR-free counterparts under the same spectral base (R:B or W), indicating a consistent inhibitory effect of reduced R:FR ratios on photosynthetic performance.

Supplementary factorial analysis (4×2 ANOVA) confirmed significant main effects of spectral base and far-red (FR) inclusion on P_n , with a significant interaction between the two factors (Supplementary Table S1). Dunnett's test further indicated that LED treatments generally increased P_n compared with the natural-light control, while *t*-tests confirmed consistently lower P_n values in FR-containing treatments across all spectral bases (Supplementary Tables S2 and S3).

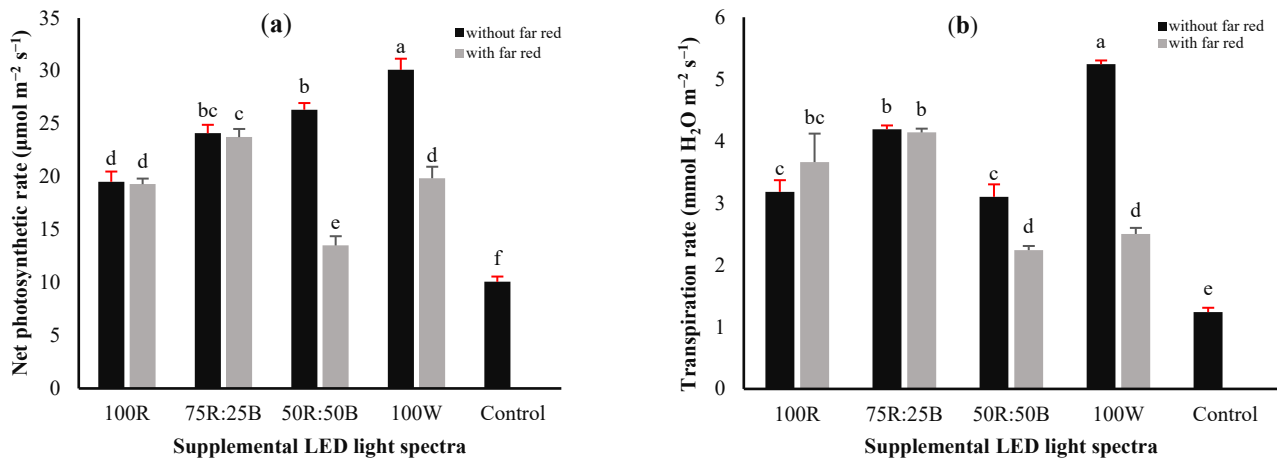


Figure 4. Effects of supplemental LED light applied at four spectral combinations (100R, 75R:25B, 50R:50B, and 100W), with or without far-red light (FR), on (a) net photosynthetic rate (Pn) and (b) transpiration rate (Tr) of potato (*S. tuberosum* L. cv. Agria). Values represent means $\pm$ SE ($n = 3$ biological replicates). Different letters indicate statistically significant differences among treatments according to Tukey's honestly significant difference (HSD) test at $p \leq 0.05$. 100R, monochromatic red; 90R+10FR, red with 10% far-red; 75R:25B, red:blue (75:25); 67R:23B+10FR, red:blue (67:23) with 10% far-red; 50R:50B, red:blue (50:50); 45R:45B+10FR, red:blue (45:45) with 10% far-red; 100W, white; 90W+10FR, white with 10% far-red; Control, natural light.

Transpiration rate (Tr) followed a similar trend (Figure 4b), with higher values recorded under 100W and red–blue combinations without FR, suggesting enhanced stomatal activity under these light conditions. FR-containing treatments exhibited consistently lower Tr values, indicating reduced stomatal conductance or altered stomatal regulation under reduced R:FR ratios. Similarly, Tr was reduced by 1.2–109.6% in FR-containing treatments compared with FR-free counterparts, indicating suppressed stomatal conductance under low R:FR conditions. Tr values were 150.0–322.6% higher under white and balanced red–blue treatments compared with the control, reflecting enhanced stomatal function under increased light availability.

Overall, treatments without FR promoted higher photosynthetic and transpiration rates, whereas FR inclusion negatively affected gas exchange performance. These results suggest that light spectral composition influences gas exchange responses through coordinated effects on stomatal behavior and photosynthetic activity, while increased light intensity acts as a primary driver of enhanced gas exchange under suboptimal irradiance conditions. Overall, gas exchange parameters varied by up to 34.1–322.6% among treatments, indicating strong spectral regulation of leaf-level physiological activity. These trends were further supported by supplementary statistical analyses, which confirmed the robustness of gas exchange responses across factorial (4×2 ANOVA), Dunnett's, and t -test comparisons (Supplementary Tables S1–S3).

3.3. Chlorophyll Content and Phenolic Compounds

Chlorophyll content and total phenolic compounds were significantly influenced by supplemental LED light spectra (Figure 5). Chlorophyll a (Chl a), chlorophyll b (Chl b), and total chlorophyll (Chl) followed similar trends across treatments (Figure 5a–c). The highest chlorophyll contents were observed under white light (100W) and balanced red–blue combinations (75R:25B and 50R:50B), indicating enhanced pigment accumulation under broad and mixed spectra. In contrast, monochromatic red light (100R) resulted in lower chlorophyll levels compared to mixed-spectrum treatments. Compared to the control, all supplemental light treatments generally exhibited higher chlorophyll content,

indicating that increased light intensity promoted pigment accumulation under low-light conditions. Chlorophyll content increased by 49.1–107.0% under white and balanced red–blue treatments compared with the control, confirming enhanced pigment accumulation under optimized spectra.

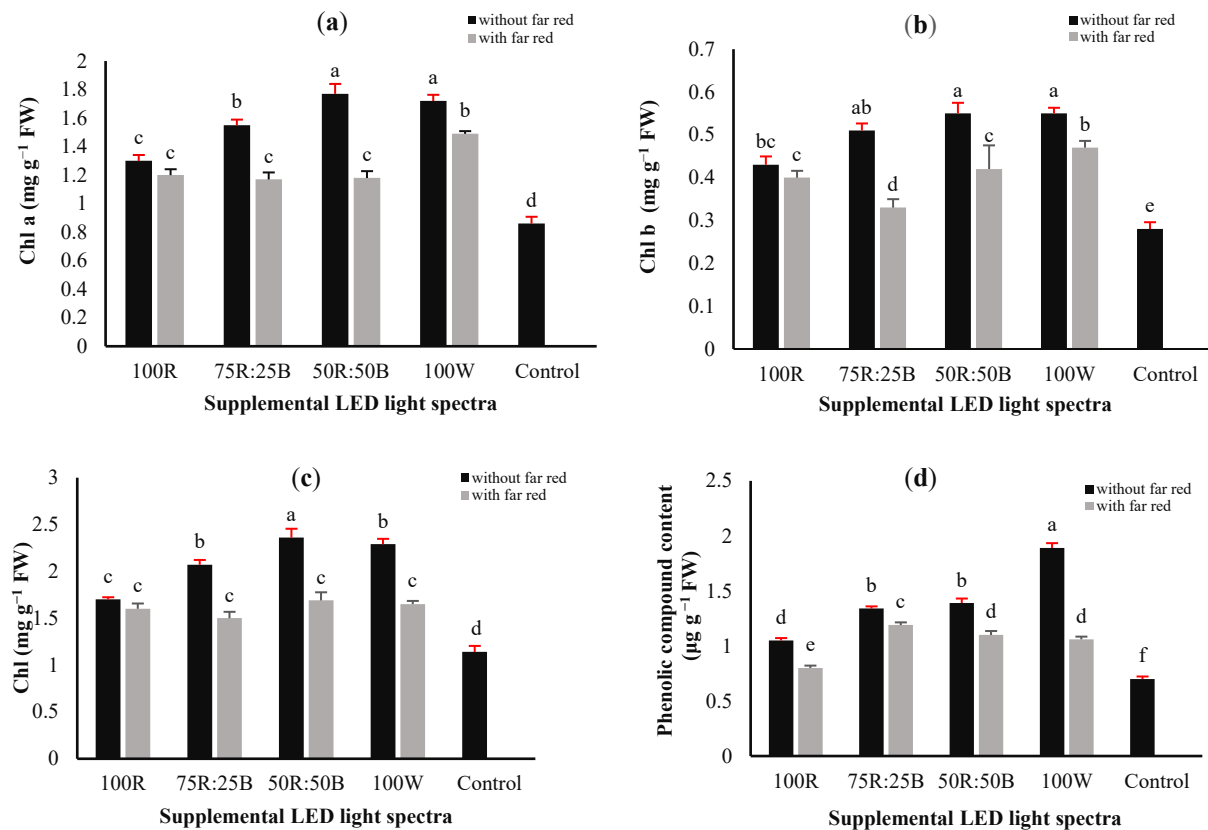


Figure 5. Effects of supplemental LED light applied at four spectral combinations (100R, 75R:25B, 50R:50B, and 100W), with or without far-red light (FR), on (a) chlorophyll a (Chl a), (b) chlorophyll b (Chl b), (c) total chlorophyll (Chl), and (d) total phenolic compounds in potato (*S. tuberosum* L. cv. Agria) leaves. Values represent means $\pm$ SE ($n = 3$ biological replicates). Different letters indicate statistically significant differences among treatments according to Tukey's honestly significant difference (HSD) test at $p \leq 0.05$. 100R, monochromatic red; 90R+10FR, red with 10% far-red; 75R:25B, red:blue (75:25); 67R:23B+10FR, red:blue (67:23) with 10% far-red; 50R:50B, red:blue (50:50); 45R:45B+10FR, red:blue (45:45) with 10% far-red; 100W, white; 90W+10FR, white with 10% far-red; Control, natural light.

FR-containing treatments consistently exhibited lower chlorophyll content across all spectral combinations. Treatments such as 90R+10FR, 67R:23B+10FR, 45R:45B+10FR, and 90W+10FR exhibited significantly lower Chl a, Chl b, and total Chl values compared to their corresponding treatments without FR, indicating that a reduced R:FR ratio was associated with lower chlorophyll content. FR inclusion reduced total chlorophyll content by 6.3–39.6% compared with FR-free counterparts across spectral combinations.

Total phenolic compounds were also significantly affected by light quality (Figure 5d). Higher phenolic accumulation was observed under balanced red–blue and white light treatments, whereas FR-containing treatments were associated with lower phenolic content. Monochromatic red light exhibited intermediate values, indicating a lower capacity to stimulate secondary metabolism compared to mixed spectra. Similarly, phenolic content was generally higher under supplemental light compared to the control, suggesting enhanced secondary metabolism under increased light availability. Total phenolic content increased by 50.0–170.0% under white and balanced red–blue treatments compared with the control.

Overall, these results indicate that light spectra without FR enhanced pigment accumulation and phenolic compound synthesis, whereas FR-containing treatments were associated with lower values of these biochemical traits, highlighting the contrasting effects of spectral composition and far-red light on plant biochemical responses. Overall, biochemical traits varied by up to 31.6–170.0% among treatments, indicating strong spectral regulation of pigment and secondary metabolite accumulation.

3.4. Vegetative Growth Responses to Light Quality

Vegetative growth parameters were significantly affected by supplemental LED light spectra (Figure 6). Leaf number, plant height, stem diameter, and shoot biomass (fresh and dry weight) showed clear responses to spectral composition and the presence of far-red light (FR). Compared to the control, plants under supplemental light generally exhibited enhanced vegetative growth, indicating that increased light intensity promoted plant development under low-light conditions. Vegetative growth traits were increased by 5.0–349.2% under supplemental light treatments compared with the control, confirming the positive effect of increased light availability on plant development.

Supplementary factorial analysis (4×2 ANOVA) confirmed significant main effects of spectral base and far-red (FR) inclusion, with a significant interaction between the two factors for plant height (Supplementary Table S1). Dunnett's test indicated that LED treatments generally enhanced growth compared with the natural-light control, while *t*-tests confirmed consistent reductions in plant height under FR-containing treatments across spectral bases (Supplementary Tables S2 and S3).

Leaf number was higher under white light (100W) and balanced red–blue combinations (75R:25B and 50R:50B), indicating enhanced leaf development under mixed spectra (Figure 6a). In contrast, FR-containing treatments were generally associated with lower leaf number across most treatments. Leaf number increased by 11.0–53.7% under white and balanced red–blue treatments compared with FR-containing treatments.

Plant height was significantly greater in FR-free treatments than in their FR-containing counterparts (Figure 6b). This response indicates that, under the light conditions applied in this study, far-red light did not trigger a classical shade-avoidance elongation response. This suggests that FR responses reflected partial phytochrome-mediated signaling rather than a full classical shade-avoidance syndrome under the present low-DLI conditions. Instead, FR-free treatments showed higher plant height values, suggesting that light intensity and spectral composition interactively regulated plant architectural development. Plant height was higher by 31.3–80.2% in FR-free treatments compared with FR-containing counterparts.

Stem diameter was greatest under 100W and red–blue combinations without FR, whereas FR-containing treatments exhibited reduced stem diameter (Figure 6c), indicating reduced stem thickness under FR treatments. Stem diameter was reduced by 17.0–47.4% under FR-containing treatments compared with FR-free counterparts.

Shoot fresh and dry weights followed similar patterns (Figure 6d,e), with the highest biomass accumulation observed under 100W and balanced red–blue treatments (75R:25B and 50R:50B). FR-containing treatments consistently exhibited lower shoot biomass, indicating that although FR promoted stem elongation, it negatively affected overall biomass accumulation. Shoot biomass (fresh and dry weight) increased by 4.5–148.3% under white and balanced red–blue treatments compared with FR-containing treatments. Overall, biomass accumulation was consistently higher under supplemental light compared to the control, highlighting the key role of increased light intensity in driving plant growth. Overall biomass accumulation increased by 5.0–349.2% under supplemental light compared with the control.

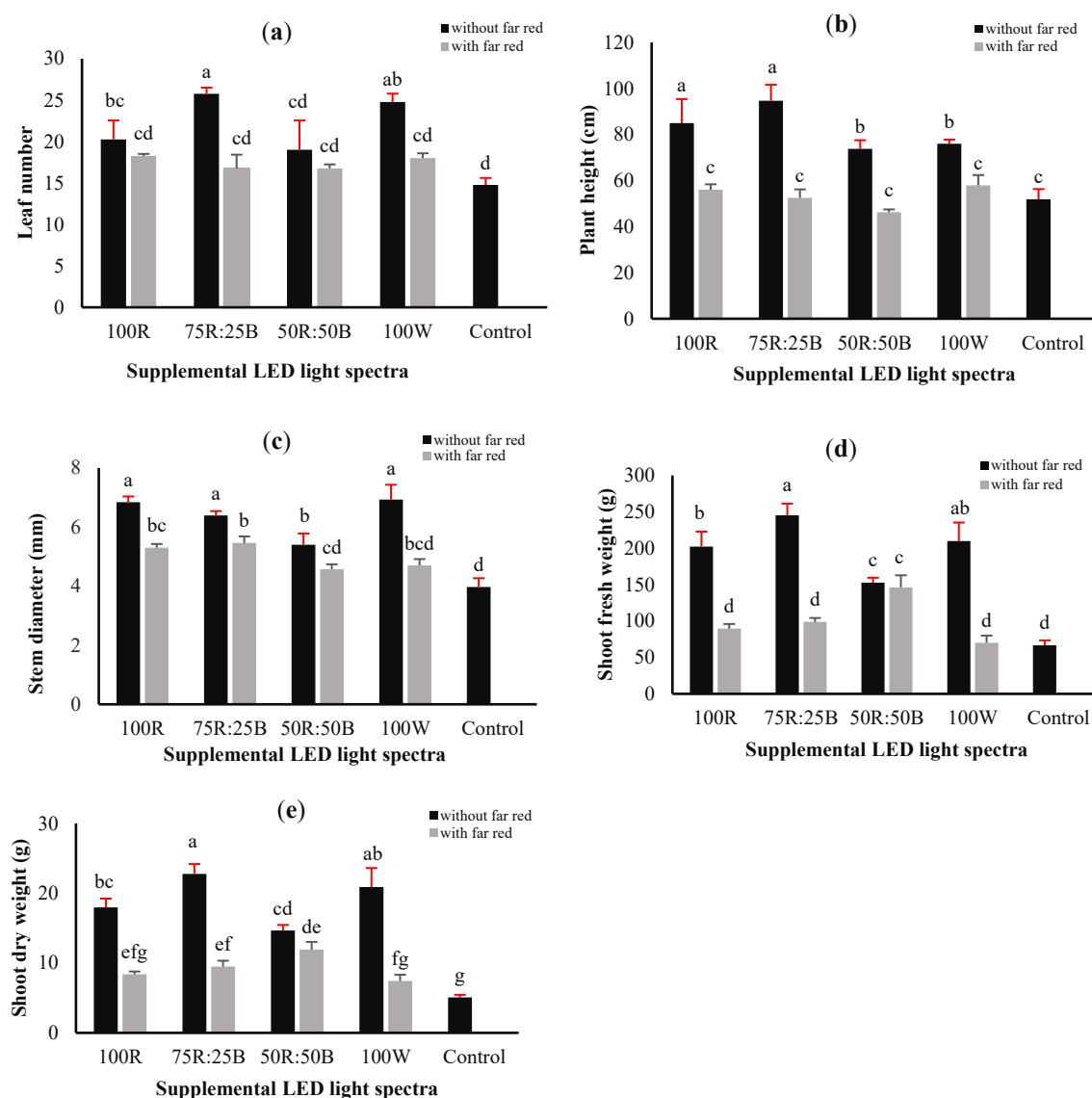


Figure 6. Effects of supplemental LED light applied at four spectral combinations (100R, 75R:25B, 50R:50B, and 100W), with or without far-red light (FR), on (a) leaf number, (b) plant height, (c) stem diameter, (d) shoot fresh weight, and (e) shoot dry weight of potato (*S. tuberosum* L. cv. Agria). Values represent means $\pm$ SE ($n = 3$ biological replicates). Different letters indicate statistically significant differences among treatments according to Tukey's honestly significant difference (HSD) test at $p \leq 0.05$. 100R, monochromatic red; 90R+10FR, red with 10% far-red; 75R:25B, red:blue (75:25); 67R:23B+10FR, red:blue (67:23) with 10% far-red; 50R:50B, red:blue (50:50); 45R:45B+10FR, red:blue (45:45) with 10% far-red; 100W, white; 90W+10FR, white with 10% far-red; Control, natural light.

Overall, treatments without FR enhanced vegetative growth and biomass production, whereas FR-containing treatments were associated with decreased elongation and reduced structural development and biomass accumulation. Overall vegetative performance varied by up to 5.0–349.2% among treatments, indicating strong spectral regulation of plant growth architecture. Overall, supplementary statistical analyses confirmed that the observed treatment effects were consistent across factorial (4×2 ANOVA), Dunnett's, and t -test comparisons (Supplementary Tables S1–S3).

3.5. Mini-Tuber Yield and Biomass Allocation

Mini-tuber yield and biomass allocation were significantly affected by supplemental LED light spectra (Figure 7). Mini-tuber number per plant was highest under white light

(100W) and balanced red–blue combinations (75R:25B and 50R:50B), indicating that mixed spectra promoted tuber initiation and development (Figure 7a). In contrast, FR-containing treatments generally exhibited lower mini-tuber numbers, indicating that a reduced R:FR ratio was associated with lower tuber formation. Mini-tuber number increased by 9.4–23.8% under white and balanced red–blue treatments compared with FR-containing treatments.

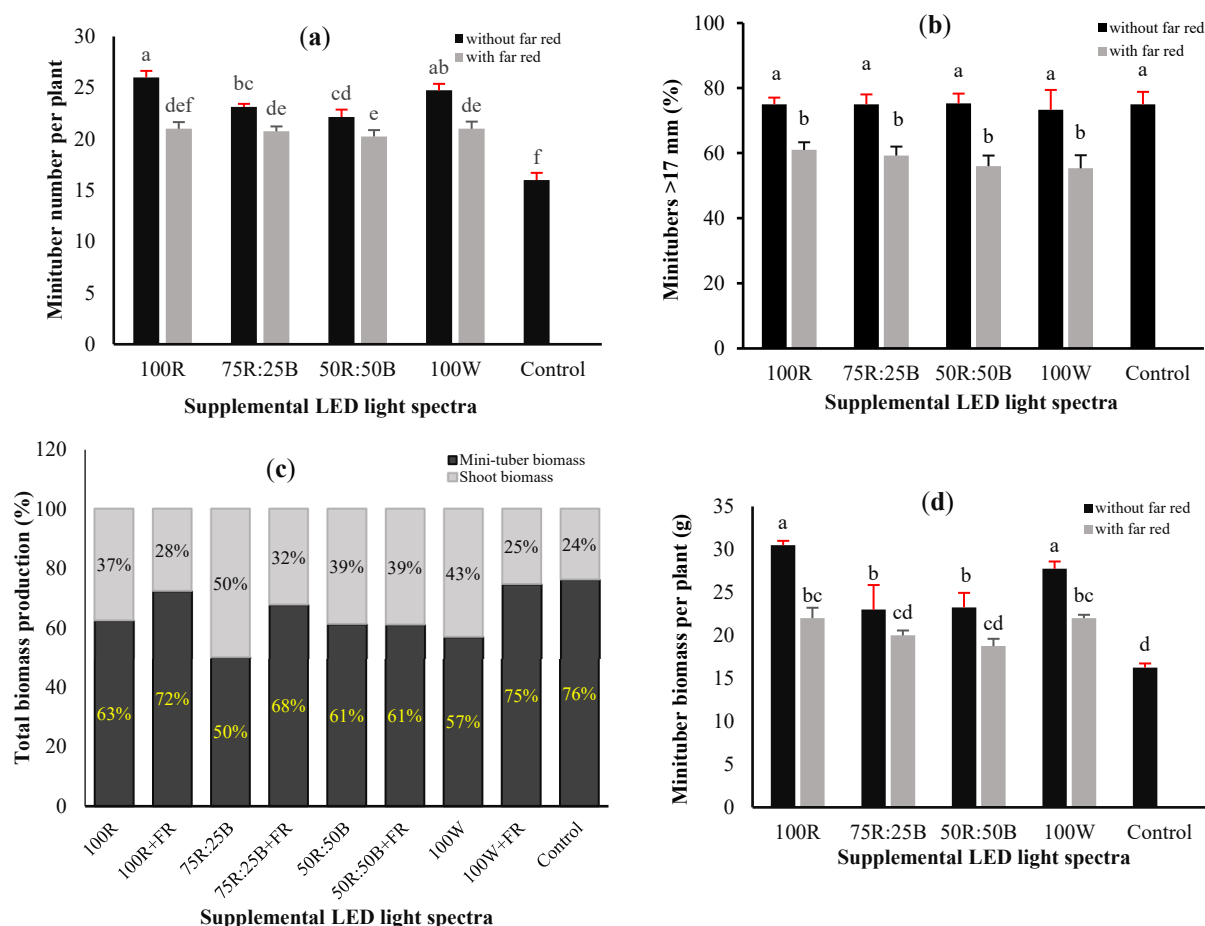


Figure 7. Effects of supplemental LED light applied at four spectral combinations (100R, 75R:25B, 50R:50B, and 100W), with or without far-red light (FR), on (a) mini-tuber number per plant, (b) percentage of mini-tubers > 17 mm, (c) total biomass per plant, and (d) mini-tuber biomass per plant of potato (*S. tuberosum* L. cv. Agria). Values represent means $\pm$ SE ($n = 3$ biological replicates). Different letters indicate statistically significant differences among treatments according to Tukey's honestly significant difference (HSD) test at $p \leq 0.05$. 100R, monochromatic red; 90R+10FR, red with 10% far-red; 75R:25B, red:blue (75:25); 67R:23B+10FR, red:blue (67:23) with 10% far-red; 50R:50B, red:blue (50:50); 45R:45B+10FR, red:blue (45:45) with 10% far-red; 100W, white; 90W+10FR, white with 10% far-red; Control, natural light.

The proportion of commercially relevant mini-tubers (>17 mm) followed a similar pattern (Figure 7b). Higher percentages were observed under 100W and red–blue combinations without FR, whereas FR-containing treatments reduced the proportion of larger tubers, suggesting reduced tuber growth and bulking under these conditions. The proportion of marketable mini-tubers increased by 23.0–32.5% under FR-free treatments compared with FR-containing treatments.

Total biomass per plant was maximized under 100W and balanced red–blue treatments (Figure 7c), reflecting enhanced overall photosynthetic performance and plant growth under these spectra. The inclusion of FR reduced total biomass, in agreement with the observed reductions in photosynthetic performance and vegetative growth. Importantly,

all supplemental light treatments resulted in higher total biomass compared to the control, indicating that increased light intensity substantially enhanced plant productivity under low-light conditions. Total biomass increased by 23.8–132.1% under supplemental light treatments compared with the control. Supplementary analyses confirmed significant effects of both spectral base and FR inclusion on total biomass, with consistent reductions observed under FR-containing treatments across spectral combinations (Supplementary Tables S1–S3).

Mini-tuber biomass per plant (Figure 7d) closely mirrored total biomass trends, with the highest values recorded under 100W and red–blue combinations without FR. Although FR treatments sometimes maintained moderate tuber biomass relative to their reduced shoot growth, overall tuber biomass remained lower compared to treatments without FR. Similarly, mini-tuber yield was consistently higher under supplemental light compared to the control, demonstrating that even moderate increases in light intensity significantly improved tuber production. Mini-tuber biomass increased by 15.0–38.6% under white and balanced red–blue treatments compared with FR-containing treatments.

Supplementary factorial analysis (4×2 ANOVA) confirmed significant effects of spectral base and far-red (FR) inclusion on mini-tuber biomass, with a significant interaction between factors (Supplementary Table S1). Dunnett's test indicated that LED treatments increased mini-tuber biomass relative to the natural-light control, while *t*-tests confirmed consistently lower tuber biomass under FR-containing treatments across spectral bases (Supplementary Tables S2 and S3).

Overall, light spectra without FR enhanced both mini-tuber yield and total biomass production, while FR inclusion reduced tuber number and size. These results indicate that light quality influenced mini-tuber productivity through coordinated effects on photosynthetic performance, plant growth, and biomass distribution to storage organs. Overall mini-tuber yield varied by 15.4–87.7% among treatments, indicating strong spectral regulation of sink strength and assimilate partitioning. Supplementary statistical analyses confirmed that these yield responses were robust across different analytical approaches (Supplementary Tables S1–S3), supporting the consistency of spectral effects across all statistical tests applied.

3.6. Pearson Correlation Analysis Among Physiological, Growth, and Yield Parameters

Pearson correlation analysis revealed strong and consistent relationships among physiological traits, vegetative growth, and mini-tuber yield (Figure 8; Supplementary Figure S2). Net photosynthetic rate (Pn) was positively correlated with shoot biomass and mini-tuber biomass, indicating that higher photosynthetic performance was associated with increased plant growth and yield formation. Similarly, the performance index on an absorption basis (PI_{abs}) was positively associated with both Pn and chlorophyll content, reflecting the association between photosynthetic efficiency and photosynthetic performance.

Chlorophyll content showed strong positive correlations with Pn and biomass accumulation, highlighting the role of pigment-mediated light capture in driving photosynthetic performance. In contrast, treatments with lower photosynthetic activity, particularly those including far-red (FR) light, were associated with reduced biomass and yield parameters, suggesting reduced photosynthetic performance and biomass production under these conditions.

Mini-tuber number and biomass were positively correlated with shoot biomass, indicating that vegetative growth and biomass accumulation were closely associated with yield formation. These relationships were consistently observed in both the core matrix (Figure 8) and the expanded dataset including additional physiological and fluorescence variables (Supplementary Figure S2), confirming the robustness of the observed associations.

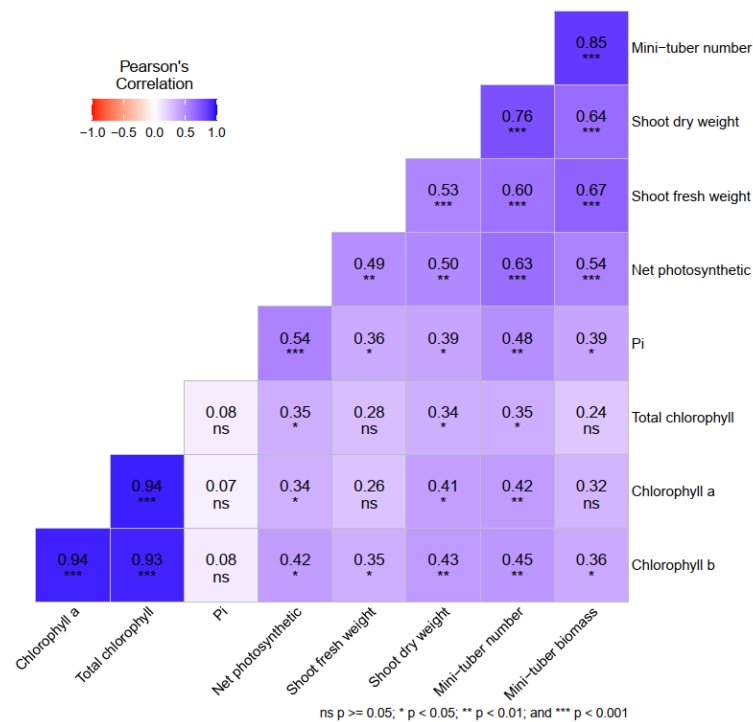


Figure 8. Pearson’s correlation matrix among key physiological, biochemical, growth, and yield parameters in potato plants under different light spectral treatments. The color scale represents correlation coefficients (r), ranging from -1 (red, negative correlation) to $+1$ (blue, positive correlation). Significant correlations are indicated by asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$), while “ns” denotes non-significant relationships ($p \geq 0.05$). The matrix highlights strong positive associations between photosynthetic performance (net photosynthesis, $PI_{a\beta s}$, chlorophyll content), shoot biomass, and mini-tuber yield traits, illustrating the associations among photosynthetic performance, vegetative growth, and mini-tuber yield traits. A more comprehensive correlation analysis including additional physiological and fluorescence parameters is provided in Supplementary Figure S2.

Overall, the correlation analysis indicates that mini-tuber production appeared to be associated with coordinated relationships among photosynthetic performance, vegetative growth, and biomass distribution, where photosynthetic performance was associated with biomass accumulation and yield formation. Light spectral composition, particularly the inclusion of far-red light, was associated with changes in the balance between photosynthetic performance and biomass distribution patterns. Correlation analysis revealed variation in the strength of associations among physiological, growth, and yield traits across treatments, highlighting strong spectral regulation of source–sink relationships. These relationships were consistent across both the main dataset (Figure 8) and the expanded correlation matrix (Supplementary Figure S2), confirming the robustness of the observed physiological–yield associations. Overall, these results emphasize that mini-tuber yield formation is tightly linked to coordinated source–sink interactions modulated by light spectral composition. These findings collectively reinforce the central role of light-mediated regulation of carbon assimilation and assimilate partitioning in determining mini-tuber productivity. Together, these results provide a coherent physiological framework linking spectral quality, carbon assimilation, and yield formation in aeroponically grown potato.

4. Discussion

4.1. Light Quality Regulates Photosynthesis Through Stomatal and Biochemical Limitations

Light spectral composition strongly influenced photosynthetic performance, primarily through coordinated effects on stomatal behavior and biochemical capacity, consistent with

the broader role of greenhouse environmental drivers in regulating physiological processes and crop performance. At the mechanistic level, these responses reflect the integration of multiple photoreceptor pathways, where blue light (via cryptochrome and phototropin signaling) primarily regulates stomatal aperture and chloroplast activation, while red light (via phytochrome signaling) modulates photosynthetic gene expression and carbon assimilation efficiency. Balanced red–blue spectra and white light appeared to promote more efficient gas exchange and photosynthetic performance, likely through improved coordination between stomatal regulation and photosynthetic activity (Figure 4a,b). This response is consistent with blue-light perception via phototropins, which activates plasma membrane H^+ -ATPase, leading to membrane hyperpolarization, K^+ uptake, and stomatal opening, thereby enhancing CO_2 diffusion into the leaf mesophyll [22]. In contrast, monochromatic red light (100R) resulted in lower Pn (Figure 4a), consistent with reports in aeroponic and greenhouse-grown potato, where the absence of blue light limits stomatal responsiveness and reduces carbon assimilation efficiency [23].

Beyond stomatal regulation, biochemical limitations likely contributed to differences in photosynthetic performance. The enhanced chlorophyll accumulation observed under balanced spectral environments suggests improved light-harvesting efficiency and excitation energy transfer to PSII (Figure 5a–c). This is supported by the higher performance index ($PI_{a\beta s}$) observed under these treatments (Figure 3d), reflecting more efficient energy conservation from photon absorption to electron transport. The stability of Fv/Fm across treatments (Figure 3c) further indicates that PSII reaction centers remained functionally intact, and that differences in Pn were not associated with photoinhibition but rather with downstream photosynthetic processes beyond primary PSII photochemistry [24]. These relationships are further supported by the positive correlations between $PI_{a\beta s}$, chlorophyll content, and Pn (Figure 8; Supplementary Figure S2), supporting a close association between photosynthetic efficiency and photosynthetic performance. Such coordinated increases indicate improved coupling between light harvesting and electron transport efficiency.

The lower Pn, $PI_{a\beta s}$, and chlorophyll content observed under far-red (FR)-containing treatments (Figures 3d, 4a and 5a–c) highlight the role of spectral balance in regulating photosynthetic efficiency. A reduced R:FR ratio shifts the phytochrome photoequilibrium toward the Pr-dominant state (lower Pfr/Pr ratio), triggering shade-avoidance signaling. This phytochrome-mediated shift induces transcriptional reprogramming that favors elongation-related growth processes (e.g., via auxin and gibberellin signaling) at the expense of photosynthetic investment and chloroplast development. This shift may be associated with reduced photosynthetic performance, as reflected by lower chlorophyll content and reduced gas exchange activity under FR-containing treatments [25]. Under the relatively low daily light integral conditions of this study (Figure 2), which are known to constrain carbon assimilation in greenhouse crops such responses may further constrain photosynthetic performance and biomass accumulation by reducing both light capture and photosynthetic capacity.

Additionally, the parallel decline in transpiration (Tr) under FR treatments (Figure 4b) suggests coordinated downregulation of stomatal conductance, further limiting CO_2 availability for photosynthesis. Overall, this indicates a multi-level regulation of carbon assimilation under modified R:FR conditions. This indicates that light quality modulates photosynthesis through an integrated control of stomatal and mesophyll processes, rather than through direct impairment of PSII photochemistry [26]. The association between reduced photosynthetic traits and lower biomass accumulation further supports the importance of maintaining sufficient photosynthetic activity and biomass production under low-light greenhouse conditions (Figure 8; Supplementary Figure S2).

Overall, these results demonstrate that light quality regulates photosynthesis through both stomatal and biochemical pathways, with blue light enhancing stomatal opening and chlorophyll accumulation, and far-red-containing treatments being associated with lower photosynthetic performance. These combined effects ultimately influence the efficiency of carbon gain under controlled environment conditions [27]. These findings are consistent with recent studies reporting multi-level regulation of photosynthetic efficiency by LED spectral composition in controlled environment systems, particularly through coordinated effects on stomatal conductance, chloroplast function, and photoreceptor signaling.

4.2. Far-Red Light Influences Biomass Allocation Patterns Consistent with Phytochrome-Mediated Signaling

FR-containing treatments altered plant architecture, but the response was not consistently indicative of classical shade-avoidance elongation. Instead, changes in stem height and diameter reflected an interaction between spectral composition and overall light availability, suggesting that FR effects were primarily mediated through photomorphogenic regulation of growth balance [28,29], associated with phytochrome photoequilibrium shifts (reduced Pfr/Pr ratio) that drive transcriptional reprogramming of elongation-associated pathways and carbon allocation networks controlling elongation-associated growth and resource allocation patterns (Figure 6b,c).

Importantly, FR-induced elongation was accompanied by reductions in shoot biomass and photosynthetic performance (Figures 4a and 6d,e), indicating a decoupling between elongation growth and overall biomass accumulation. This decoupling reflects a fundamental trade-off between phytochrome-mediated elongation signaling and carbon assimilation capacity, where resources are preferentially allocated to stem expansion at the expense of photosynthetic apparatus maintenance and biomass accumulation. While elongation may enhance light interception under competitive canopies, under controlled aeroponic conditions with non-limiting spacing it represents a maladaptive allocation strategy [30]. These responses suggest a preferential promotion of elongation-related growth processes (e.g., cell expansion and stem elongation) rather than biomass accumulation, leading to reduced structural development and overall productivity [31].

At the physiological level, FR also reduced chlorophyll content and phenolic compounds (Figure 5a–d), indicating broader physiological and metabolic adjustments. Reduced chlorophyll levels suggest reduced photosynthetic capacity and light-harvesting potential, consistent with the decline in $PI_{a\beta s}$ (Figure 3d) and net photosynthetic rate (Figure 4a) [30]. Simultaneously, the decrease in phenolic compounds reflects a shift away from secondary metabolism, which is often associated with photoprotection and defense, toward primary growth processes [32]. This shift reflects a coordinated reprogramming of carbon allocation and redox balance, whereby reduced investment in secondary metabolism coincides with enhanced allocation toward structural elongation growth under low R:FR conditions. The supplementary factorial analysis confirmed that both spectral composition and far-red light, as well as their interaction, contributed to the observed physiological responses, supporting the interpretation that FR effects are context-dependent rather than isolated single-factor effects (Supplementary Table S1). These coordinated physiological responses are consistent with phytochrome-mediated signaling, which may prioritize rapid elongation over resource-intensive processes such as pigment synthesis and secondary metabolism [33].

Furthermore, the reduction in transpiration (Tr) under FR treatments (Figure 4b) suggests coordinated modulation of stomatal function, associated with hormonal signaling (e.g., auxin and potential hormonal interactions) under low R:FR conditions. This further constrains carbon assimilation and reinforces the reduced photosynthetic performance observed under FR-containing treatments [34]. The observed association between reduced

photosynthetic performance and lower biomass accumulation supports the hypothesis that FR-mediated signaling may favor elongation-related growth responses over biomass accumulation and photosynthetic performance under low-light greenhouse conditions.

Collectively, these results suggest that FR light modulates carbon allocation patterns through phytochrome-mediated signaling networks that promote elongation-driven growth at the expense of photosynthetic investment, thereby reducing carbon assimilation efficiency and mini-tuber productivity under low-light greenhouse conditions.

4.3. Linking Carbon Assimilation to Mini-Tuber Formation and Yield

The reduced photosynthetic performance observed under FR-containing treatments may help explain the lower mini-tuber yield observed under these treatments (Figure 7), linking spectral signaling with altered relationships between vegetative growth and storage organ development.

Mini-tuber yield appeared to be closely associated with the balance between photosynthetic performance and biomass distribution patterns, in agreement with previous findings highlighting the dominant role of preharvest environmental conditions in determining crop performance and product quality. Treatments promoting more efficient photosynthetic performance and photochemical activity were also associated with enhanced mini-tuber formation and biomass accumulation (Figure 7a–d). In contrast, monochromatic red light (100R) resulted in intermediate performance, consistent with its lower Pn compared to mixed spectra (Figure 4a). The association among higher Pn and Tr, increased chlorophyll content, and elevated $PI_{a\beta s}$ suggests that improved light capture and electron transport supported conditions associated with enhanced tuber initiation and bulking. This relationship is further supported by the strong positive correlations among Pn, chlorophyll content, biomass, and mini-tuber yield (Figure 8; Supplementary Figure S2), supporting the proposed importance of photosynthetic performance in productivity regulation. Under aeroponic conditions, where root-zone constraints are minimized, this increase in photosynthetic performance and biomass accumulation appears to be the dominant determinant of yield [35].

In contrast, FR-containing treatments consistently reduced total biomass and mini-tuber yield (Figure 7c,d), despite sometimes maintaining comparable or slightly higher allocation ratios to tubers relative to shoots. This pattern is consistent with altered relationships between vegetative growth and storage organ development: phytochrome-mediated low R:FR signaling may alter assimilate partitioning signals and developmental cues for allocation [16], but the concurrent reduction in photosynthetic performance (lower Pn, $PI_{a\beta s}$, and pigment levels; Figures 3–5) limits overall biomass production potential. Consequently, altered biomass distribution patterns cannot compensate for reduced photosynthetic performance and biomass production, resulting in lower final yield [36]. This reduction in yield likely reflects constrained assimilate supply (particularly sucrose availability) to developing tubers, thereby limiting sink strength and tuber bulking under FR conditions.

According to previous studies, tuberization depends on the integration of carbon status with signaling pathways controlling sink initiation (e.g., sucrose signaling and hormonal regulation) [14]. The superior performance of white light likely arises from its broad spectrum, which simultaneously supports efficient photosynthesis and balanced activation of photoreceptors, stabilizing both photosynthetic activity and storage organ development [16]. Likewise, R:B combinations optimize the trade-off between light absorption (red-driven excitation) and stomatal and photomorphogenic control (blue-light effects), enhancing both photosynthetic performance and biomass accumulation associated with storage organ growth [37].

Overall, these results demonstrate that mini-tuber formation is governed by an integrated source–sink framework (Figure 7), where light quality appears to influence not only overall photosynthetic performance but also biomass distribution patterns between vegetative tissues and storage organs, reinforcing the concept that environmental drivers during cultivation shape productivity outcomes in a species-specific manner [37]. Importantly, the results also highlight that increased light intensity through supplemental lighting enhanced overall photosynthetic performance, biomass accumulation, and yield, while spectral composition and FR inclusion modulated biomass distribution patterns between vegetative tissues and storage organs. This interpretation is further strengthened by the supplementary statistical analyses, which consistently indicated coordinated effects of spectral base and far-red inclusion on growth and yield traits (Supplementary Tables S1–S3). The 4×2 ANOVA further confirmed significant main effects of spectral base and FR, as well as their interaction, on key yield-related traits, consistent with the Dunnett and *t*-test analyses. Under the relatively low DLI conditions of this study (Figure 2), enhanced photosynthetic performance and biomass production were key determinants of productivity, together with coordinated source–sink regulation controlling assimilate partitioning.

Gas exchange measurements were performed during a defined morning period (09:00–11:00 h) under representative and relatively stable greenhouse conditions and were intended primarily to provide comparative physiological responses among treatments rather than estimates of whole-day carbon assimilation. Although measurements were conducted on representative days and within a narrow temporal window to minimize environmental variability, fluctuations in natural irradiance during the day mean that instantaneous measurements may not fully capture integrated daily carbon gain. Therefore, the relationships observed between photosynthetic traits and biomass accumulation should be interpreted as indicative associations rather than definitive evidence of causal relationships between photosynthetic performance and yield formation. Nevertheless, the consistency between physiological responses and cumulative biomass and mini-tuber production supports the biological relevance of the observed treatment effects.

4.4. Limitations and Outlook

While this study provides clear evidence that light spectral composition regulates physiological processes and mini-tuber production, several limitations should be considered. First, the experiment was conducted under a single supplemental light intensity and relatively stable environmental conditions; thus, interactions between spectral quality and other key drivers such as light intensity (DLI), temperature, and vapor pressure deficit were not explored. In addition, the experiment was conducted during a single growing cycle; therefore, repeating the study across multiple experimental cycles and seasons would be important to verify the consistency, reproducibility, and robustness of the observed spectral responses. Given that light intensity strongly influenced photosynthetic performance, biomass accumulation, and yield under the low-DLI conditions of this study, further investigation of intensity–spectrum interactions is particularly important. FR effects are highly context-dependent, particularly under low versus high irradiance; therefore, the responses observed here may differ under alternative environmental scenarios (Figure 2), as also highlighted for greenhouse systems under variable climates. Because FR photons partially replaced PAR photons in FR treatments, the observed responses may reflect the combined effects of reduced R:FR ratio and modestly reduced PAR supply, rather than phytochrome-mediated FR signaling alone. Because the experiment was conducted under greenhouse conditions with fluctuating natural irradiance, the canopy-level spectral environment reflected the interaction between solar and supplemental lighting. Therefore, some

responses attributed to spectral quality may also reflect the combined effects of spectral composition and variation in overall light availability between treatments.

Second, the study was based on a single cultivar ('Agria'), and genotype-specific variation in light perception, photosynthetic capacity, and tuberization responses may influence the generality of these findings. Third, although physiological parameters such as gas exchange, chlorophyll fluorescence, and biochemical traits were comprehensively assessed (Figures 3–5), the underlying molecular and hormonal mechanisms, particularly those related to phytochrome signaling, carbohydrate transport, and sink regulation, were not directly quantified. Direct measurements of Rubisco activity, chloroplast ultrastructure, leaf nitrogen status, and biochemical photosynthetic limitations were not performed. In addition, soluble sugars, sucrose, starch, and non-structural carbohydrate dynamics were not directly quantified; therefore, carbon movement and biomass distribution processes were inferred indirectly from physiological and biomass allocation responses. Accordingly, the proposed source–sink interpretation framework should be interpreted as a conceptual physiological model integrating measured responses with hypothesized signaling mechanisms.

Future research should address the interaction between spectral composition and light intensity, especially under dynamic greenhouse conditions where natural light fluctuates. Incorporating time-resolved measurements (e.g., diel photosynthetic responses and carbohydrate dynamics) would help to better characterize relationships between photosynthetic performance, biomass accumulation, and storage organ development under different spectra. Because gas exchange measurements were conducted under ambient treatment-specific light environments rather than standardized chamber irradiance conditions, the observed Pn responses reflect both physiological acclimation and instantaneous spectral/light effects during measurement. In addition, integrating molecular approaches, including analysis of phytochrome-mediated signaling pathways, sugar sensing, and hormone regulation (e.g., auxin and gibberellins), would provide stronger mechanistic insight into how light quality may regulate biomass distribution patterns and tuber development. Combining these approaches with integrative analyses and modeling frameworks could further strengthen the interpretation of source–sink relationships under varying light environments.

Finally, evaluating multiple cultivars and tailoring spectral strategies to specific developmental stages (e.g., vegetative growth vs. tuber initiation and bulking) could further optimize aeroponic mini-tuber production systems. Such approaches would support the development of precision lighting strategies that maximize both resource-use efficiency and yield under controlled environment agriculture, in line with the need for climate-adaptive greenhouse management.

The consistency of the observed responses across one-way ANOVA and supplementary factorial, Dunnett's, and *t*-test analyses further supports the robustness of the observed treatment effects, particularly regarding spectral base and far-red inclusion.

5. Conclusions

Light spectral composition strongly influenced photosynthetic performance, biomass distribution patterns, and mini-tuber production in aeroponic potato. In addition, increasing light intensity through supplemental lighting significantly enhanced photosynthetic performance, plant growth, and yield under low-light conditions. White light (100W) and balanced red–blue spectra (75R:25B and 50R:50B) enhanced photosynthetic performance, plant growth, and yield, whereas far-red (FR)-containing treatments were associated with reduced photosynthetic performance and biomass accumulation despite promoting elongation growth.

White and balanced red–blue spectra were associated with higher photosynthetic performance, biomass accumulation, and mini-tuber yield, whereas FR-containing spectra promoted elongation and reduced yield under the tested conditions.

Overall, these results suggest that optimizing light spectra to maximize photosynthetic performance is important for improving aeroponic mini-tuber production, while ensuring sufficient light availability to sustain biomass accumulation and yield, with white and balanced red–blue light providing the most effective strategy under the tested conditions. These conclusions apply specifically to *S. tuberosum* L. cv. Agria grown under the low-light greenhouse and aeroponic conditions was evaluated in the present study.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/horticulturae12060690/s1>. Supplementary Figure S1. Schematic representation of the effects of nine LED light treatments (100R, 90R+10FR, 75R:25B, 67R:23B+10FR, 50R:50B, 45R:45B+10FR, 100W, 90W+10FR, and Control) on potato plants grown in an aeroponic system. The light spectra influenced chlorophyll fluorescence parameters (F_0 , F_m , F_v/F_m , $PI_{a\beta s}$), gas exchange traits (P_n , Tr), biochemical characteristics (chlorophyll a, chlorophyll b, total chlorophyll, total phenolics), vegetative growth (leaf number, plant height, stem diameter, shoot fresh and dry biomass), and mini-tuber production (tuber number, marketable mini-tubers > 17 mm, total biomass, and mini-tuber biomass). Supplementary Figure S2. Pearson’s correlation matrix among physiological, biochemical, growth, and yield parameters of potato plants under different light spectral treatments. The color scale represents Pearson’s correlation coefficients (r), ranging from -1 (strong negative; red) to $+1$ (strong positive; blue). Significant correlations are indicated by asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$), while “ns” denotes non-significant relationships ($p \geq 0.05$). The expanded matrix includes chlorophyll fluorescence parameters (F_0 , F_m , F_v/F_m), gas exchange traits, biochemical variables, vegetative growth traits, and mini-tuber yield components, providing a comprehensive overview of trait interrelationships. Supplementary Table S1. Two-way analysis of variance (ANOVA) for selected physiological, growth, and yield traits of aeroponically grown potato. Values represent mean squares (MS) for the effects of spectral base, far-red (FR) light, and their interaction. The analyzed traits include net photosynthetic rate (P_n), performance index on absorption basis ($PI_{a\beta s}$), total biomass, mini-tuber biomass, and plant height. Significant effects are indicated as ** ($p \leq 0.01$), * ($p \leq 0.05$), and ns ($p > 0.05$). Supplementary Table S2. Comparison of supplemental LED spectral treatments relative to the natural-light control. Data represent percentage (%) differences in treatment means compared to the control for net photosynthetic rate (P_n), performance index on an absorption basis ($PI_{a\beta s}$), total biomass, mini-tuber biomass, and plant height of aeroponically grown potato. Statistical significance was determined using Dunnett’s multiple comparison test, with p-values adjusted for multiple comparisons. Significant differences from the control are indicated at $p \leq 0.05$. “+FR treatments” refers to spectral treatments supplemented with $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ far-red light added to the base spectra. Supplementary Table S3. Results of independent samples t -tests comparing far-red (FR)-containing and FR-free treatments within each spectral base. The analyzed traits include net photosynthetic rate (P_n), performance index on an absorption basis ($PI_{a\beta s}$), total biomass, mini-tuber biomass, and plant height of aeroponically grown potato. Values represent p-values from independent samples t -tests comparing FR-containing (+FR) and FR-free treatments within each spectral base. Statistical significance is indicated at $p \leq 0.05$.

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Abbreviations

B, blue light; Chl, chlorophyll; Chl a, chlorophyll a; Chl b, chlorophyll b; DLI, daily light integral; DW, dry weight; EC, electrical conductivity; FR, far-red light; FW, fresh weight; HPLC, high-performance liquid chromatography; LED, light-emitting diode; PAR, photosynthetically active radiation; Pn, net photosynthetic rate; R, red light; R:B, red to blue light ratio; R:FR, red to far-red light ratio; RH, relative air humidity; Tr, transpiration rate; UV, ultraviolet; W, white light.

References

1. Cioloca, M.; Tican, A.; Popa, M. Evaluation of virus-free potato minitubers derived from in vitro meristem cultures for high-quality seed potato production. *Rom. J. Hortic.* **2024**, *5*, 15–22. [\[CrossRef\]](#)
2. Buckseth, T.; Tiwari, J.K.; Singh, R.K.; Kumar, V.; Sharma, A.K.; Dalamu, D.; Bhardwaj, V.; Sood, S.; Kumar, M.; Sadawarti, M.; et al. Advances in innovative seed potato production systems in India. *Front. Agron.* **2002**, *4*, 956667. [\[CrossRef\]](#)
3. Rahman, M.H.; Islam, M.J.; Mumu, U.H.; Ryu, B.R.; Lim, J.D.; Azad, M.O.K.; Cheong, E.J.; Lim, Y.S. Effect of light quality on seed potato (*Solanum tuberosum* L.) tuberization when aeroponically grown in a controlled greenhouse. *Plants* **2024**, *13*, 737. [\[CrossRef\]](#) [\[PubMed\]](#)
4. Fanourakis, D.; Makraki, T.; Vlachogiannakis, E.; Tsaniklidis, G.; Körner, O.; Ntatsi, G. Innovations in Agronomy and Their Impact on Greenhouse Vegetable Yields: Species-Specific Perspectives. *Horticulturae* **2026**, *12*, 684. [\[CrossRef\]](#)
5. Mawphlang, O.I.L.; Kharshiing, E.V. Photoreceptor mediated plant growth responses: Implications for photoreceptor engineering toward improved performance in crops. *Front. Plant Sci.* **2017**, *8*, 1181. [\[CrossRef\]](#)
6. Fanourakis, D.; Tsaniklidis, G.; Makraki, T.; Nikoloudakis, N.; Bartzanas, T.; Sabatino, L.; Fatnassi, H.; Ntatsi, G. Climate change impacts on greenhouse horticulture in the Mediterranean basin: Challenges and adaptation strategies. *Plants* **2025**, *14*, 3390. [\[CrossRef\]](#) [\[PubMed\]](#)
7. Zheng, L.; He, H.; Song, W. Application of light-emitting diodes and the effect of light quality on horticultural crops: A review. *HortScience* **2010**, *45*, 1656–1661. [\[CrossRef\]](#)
8. Mascoli, V.; Bersanini, L.; Croce, R. Far-red absorption and light-use efficiency trade-offs in chlorophyll f photosynthesis. *Nat. Plants* **2020**, *6*, 1044–1053. [\[CrossRef\]](#)
9. Yang, D.; Seaton, D.D.; Krahmer, J.; Halliday, K.J. Photoreceptor effects on plant biomass, resource allocation, and metabolic state. *Proc. Natl. Acad. Sci. USA* **2016**, *113*, 7667–7672. [\[CrossRef\]](#)
10. Fanourakis, D.; Körner, O.; Makraki, T.; Spyrou, G.P.; Karavidas, I.; Tsaniklidis, G.; Woltering, E.; Ntatsi, G. Greenhouse climate shapes nitrate levels, nutritional quality, and shelf life in leafy vegetables: Species-specific responses. *Front. Plant Sci.* **2026**, *17*, 1806482. [\[CrossRef\]](#)
11. Fanourakis, D.; Makraki, T.; Spyrou, G.P.; Karavidas, I.; Tsaniklidis, G.; Ntatsi, G. Environmental drivers of fruit quality and shelf life in greenhouse vegetables: Species-specific insights. *Agronomy* **2026**, *16*, 48. [\[CrossRef\]](#)
12. Khan, T.A.; Mundra, S.; Gururani, M.A. Advancements in Photosynthetic Efficiency: Pathways, Regulation, and Biotechnological Applications for Enhancing Crop Productivity. *Plant Signal. Behav.* **2025**, *20*, 2596483. [\[CrossRef\]](#)
13. Lehretz, G.G.; Sonnewald, S.; Sonnewald, U. Assimilate highway to sink organs—Physiological consequences of SP6A overexpression in transgenic potato (*Solanum tuberosum* L.). *J. Plant Physiol.* **2021**, *266*, 153530. [\[CrossRef\]](#)
14. Singh, P.; Arif, Y.; Siddiqui, H.; Upadhyaya, C.P.; Pichtel, J.; Hayat, S. Critical factors responsible for potato tuberization. *Bot. Rev.* **2023**, *89*, 421–437. [\[CrossRef\]](#)
15. Ryu, K.O.; Shin, E.J.; Lee, S.; Lee, J.G.; Cha, E.B.; Sunwoo, Y.; Hong, J.; Yoon, J.E.; Lee, J.H.; Nam, S.Y. Spectral Modulation of Morphophysiological Responses and Plant Quality in Korean White Dandelion (*Taraxacum coreanum* Nakai) Under Controlled Environmental Conditions. *Agriculture* **2026**, *16*, 830. [\[CrossRef\]](#)
16. He, W.; Li, J.; Pu, M.; Xu, Z.G.; Gan, L. Response of photosynthate distribution in potato plants to different LED spectra. *Funct. Plant Biol.* **2020**, *47*, 1128–1137. [\[CrossRef\]](#)

17. Pundir, R.K.; Pathak, A.; Joshi, N.; Bagri, D.S.; Upadhyaya, C.P. Irradiation studies of LED light spectra on the growth and development of potato (*Solanum tuberosum* L.). *Plant Sci. Today* **2020**, *7*, 406–416. [\[CrossRef\]](#)
18. Aalam, F.; Rezaei Nejad, A.; Mousavi-Fard, S.; Raji, M.; Nikoloudakis, N.; Goumenaki, E.; Fanourakis, D. Water Deficit Severity during the Preceding Year Determines Plant Tolerance to Subsequent Year Drought Stress Challenges: A Case Study in Damask Rose. *Horticulturae* **2024**, *10*, 462. [\[CrossRef\]](#)
19. Lichtenthaler, H.K. Chlorophylls and carotenoids: Pigments of photosynthetic biomembranes. *Methods Enzymol.* **1987**, *148*, 350–382.
20. Jung, H.J.; Kim, J.H.; Davaatseren, M. Antioxidant and phenolic contents in potatoes (*Solanum tuberosum* L.) and micropropagated potatoes. *Appl. Biol. Chem.* **2019**, *62*, 17. [\[CrossRef\]](#)
21. Tsaniklidis, G.; Makraki, T.; Papadimitriou, D.; Nikoloudakis, N.; Taheri-Garavand, A.; Fanourakis, D. Non-destructive estimation of area and greenness in leaf and seedling scales: A case study in cucumber. *Agronomy* **2025**, *15*, 2294. [\[CrossRef\]](#)
22. Yavari, N.; Tripathi, R.; Wu, B.-S.; MacPherson, S.; Singh, J.; Lefsrud, M. The effect of light quality on plant physiology, photosynthetic, and stress response in *Arabidopsis thaliana* leaves. *PLoS ONE* **2021**, *16*, e0247380. [\[CrossRef\]](#) [\[PubMed\]](#)
23. Bernardo, E.L.; Sales, C.R.G.; Cubas, L.A.; Vath, R.L.; Kromdijk, J. A comparison of stomatal conductance responses to blue and red light between C3 and C4 photosynthetic species in three phylogenetically controlled experiments. *Front. Plant Sci.* **2023**, *14*, 1253976. [\[CrossRef\]](#) [\[PubMed\]](#)
24. Gunell, S.; Lempiäinen, T.; Rintamäki, E.; Aro, E.M.; Tikkanen, M. Enhanced function of non-photoinhibited photosystem II complexes upon PSII photoinhibition. *Biochim. Biophys. Acta Bioenerg.* **2023**, *1864*, 148978. [\[CrossRef\]](#) [\[PubMed\]](#)
25. Li, Y.; Zhao, J.; Ma, H.; Pu, L.; Zhang, J.; Huang, X.; Yang, H.; Fan, G. Shade tolerance in wheat is related to photosynthetic limitation and morphological and physiological acclimations. *Front. Plant Sci.* **2024**, *15*, 1465925. [\[CrossRef\]](#)
26. Park, J.U.; An, S.K.; Kim, J. Far-red light affects stomatal opening and evapotranspiration of sweet basil. *Horticulturae* **2023**, *9*, 1095. [\[CrossRef\]](#)
27. Gustavsson, M.; Hill, L.; Franklin, K.A.; Pridgeon, A.J. Integration of light quality signals regulates ABA abundance and stomatal movements during seedling establishment. *New Phytol.* **2025**, *249*, 1253–1267. [\[CrossRef\]](#)
28. Ballare, C.L.; Pierik, R. The shade-avoidance syndrome: Multiple signals and ecological consequences. *Plant Cell Environ.* **2017**, *40*, 2530–2543. [\[CrossRef\]](#)
29. Sharma, A.; Pridgeon, A.J.; Liu, W.; Segers, F.; Sharma, B.; Jenkins, G.I.; Franklin, K.A. Elongated hypocotyl 5 (HY5) and HY5 homologue (HYH) maintain shade avoidance suppression in UV-B. *Plant J.* **2023**, *115*, 1394–1407. [\[CrossRef\]](#)
30. Leschevin, M.; Ksas, B.; Baltenweck, R.; Huguene, P.; Caffarri, S.; Havaux, M. Photosystem rearrangements, photosynthetic efficiency, and plant growth in far red-enriched light. *Plant J.* **2024**, *120*, 2536–2552. [\[CrossRef\]](#)
31. Körner, C. Paradigm shift in plant growth control. *Curr. Opin. Plant Biol.* **2015**, *25*, 107–114. [\[CrossRef\]](#)
32. Su, P.; Ding, S.; Wang, D.; Kan, W.; Yuan, M.; Chen, X.; Tang, C.; Hou, J.; Wu, L. Plant morphology, secondary metabolites and chlorophyll fluorescence of *Artemisia argyi* under different LED environments. *Photosynth. Res.* **2024**, *159*, 153–164. [\[CrossRef\]](#)
33. Zhang, Y.; Wang, S.; Li, J. Light regulates the synthesis and accumulation of plant secondary metabolites. *Front. Plant Sci.* **2025**, *16*, 1644472. [\[CrossRef\]](#)
34. Gómez-Ocampo, G.; Cascales, J.; Medina-Fraga, A.L.; Ploschuk, E.L.; Mantese, A.I.; Crocco, D.; Matsusaka, C.D.; Sánchez, D.H.; Botto, J.F. Transcriptomic and physiological shade avoidance responses in potato (*Solanum tuberosum*) plants. *Physiol. Plant.* **2023**, *175*, e13991. [\[CrossRef\]](#)
35. Zinta, R.; Tiwari, J.K.; Buckseth, T.; Goutam, U.; Singh, R.K.; Thakur, A.K.; Kumar, M. Agro-physiological and transcriptome profiling reveal key genes associated with potato tuberization under different nitrogen regimes in aeroponics. *PLoS ONE* **2025**, *20*, e0320313. [\[CrossRef\]](#) [\[PubMed\]](#)
36. Katoh, A.; Ashizawa, T.; Kasai, M. Potato yield enhancement through intensification of sink and source performances. *Breed. Sci.* **2015**, *65*, 77–84. [\[CrossRef\]](#) [\[PubMed\]](#)
37. Li, X.; Zhao, S.; Lin, A.; Yang, Y.; Zhang, G.; Xu, P.; Wu, Y.; Yang, Z. Effect of different ratios of red and blue light on maximum stomatal conductance and response rate of cucumber seedling leaves. *Agronomy* **2023**, *13*, 941. [\[CrossRef\]](#)

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