

Article

LED-Driven Rapid Generation in Soybean: Photoperiod and Spectral Effects

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Abstract

This study evaluated LED-supported speed-breeding conditions for two registered soybean cultivars ('Sonya' and 'Victoria'; approximately Maturity Groups III–IV) by testing four constant photoperiod regimes (10, 14, 18, and 22 h light) combined with four LED spectral treatments differing in high red (HR; 640–660 nm), deep blue (DB; 450–460 nm), far-red (FR; 720–730 nm), cool white (CW; 6500 K; 400–700 nm) and warm white (WW; 3000 K; 400–700 nm) components. Photoperiod treatments were implemented as sequential runs in a controlled growth-chamber (28 ± 2 °C; $\geq 50\%$ RH; $400\text{--}600 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD), and performance was compared with a field trial in Antalya, Türkiye. Developmental timing (R1, R6), plant height, stem dry weight, pod number, seed oil concentration, fatty acid composition, and seed germination were analyzed using mixed-effects and generalized linear mixed models. Photoperiod exerted dominant control over developmental timing. The 10 h photoperiod regime produced the fastest progression (R1 $\approx$ 24.5 DAS; R6 $\approx$ 50 DAS), whereas 18 h markedly delayed R1 and R6 (with one LED treatment within 18 h failing to reach R6), and 22 h did not reach R6. LED spectral treatment did not affect R1 or R6 within photoperiods, but influenced plant height, stem dry weight, total seed oil, and germination. Field-grown plants produced substantially higher biomass and pod number than growth chamber-grown plants, consistent with greater branching and pod set under open-field, direct-sown conditions. Total seed oil concentration differed by environment and cultivar with no environment $\times$ cultivar interaction, while centered log-ratio PERMANOVA indicated largely stable fatty acid proportional composition across environments and LED treatments. Germination analyses (restricted to 10 h and 14 h due to insufficient seed production) showed significant effects of LED treatment and harvest timing, with the highest germination under LED-3. Overall, our results indicate that a constant 10 h photoperiod, combined with immature seed harvest from approximately R6 + 20 onward, provides an effective strategy for accelerating soybean generation turnover while maintaining high germination capacity. LED spectral design can also be used to modulate plant architecture and seed quality without substantially altering developmental timing.



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1. Introduction

Soybean (*Glycine max* L.), a facultative short-day plant, is the most widely cultivated legume globally and consistently ranks fourth among the world's most produced crops after wheat, rice, and maize [1]. Owing to its high protein and oil content, soybean is extensively utilized in feed, food, pharmaceutical, and industrial applications [2–4]. With the global population projected to reach approximately 10 billion by 2050, the demand for high-yielding, nutritionally dense, and climate-resilient soybean cultivars is intensifying [5,6]. In parallel, controlled environment agriculture (CEA) and plant factories are increasingly recognized as strategic platforms for securing year-round, resource-efficient crop production capacity [7,8]. Compounding this pressure, climate change-induced stresses—including rising temperatures, flooding, emerging pests and diseases, drought, and irregular precipitation—necessitate accelerated genetic improvement to sustain soybean productivity [6].

Conventional soybean breeding has successfully produced improved cultivars; however, progress remains slow due to long generation times, dependence on field-based selection, and strong environmental influences on phenotypic expression [9]. Under natural conditions, soybean typically completes only one generation as a summer crop [10], and cultivar development from initial crossing to release may require 8–10 years. These limitations underscore the need for approaches that shorten breeding cycles and accelerate genetic gain, particularly under controlled environments where key developmental drivers can be precisely manipulated.

Plant breeding pipelines increasingly integrate a range of strategies and tools, including classical line-development approaches such as single-seed descent and doubled haploid production [11], together with enabling platforms and modern molecular technologies including biotron-based breeding systems [12,13], marker-assisted selection [14], genomic selection [15], and genome editing [16,17]. While effective, their broad deployment is often constrained by cost, technical complexity, infrastructure requirements, and crop-specific or regulatory limitations [16]. Consequently, there is increasing demand for scalable strategies that are economically feasible, operationally straightforward, and readily integrated into established breeding pipelines.

Speed breeding (SB), first systematically described by Watson et al. [18], accelerates crop improvement by optimizing environmental factors such as photoperiod, light spectrum, and temperature, often coupled with early seed harvest [5]. Thermal management can accelerate floral development, seed fill, and maturation [17], and photoperiod modulates phytochrome-mediated signaling pathways that govern germination and flowering [19]. In long-day crops, SB has achieved notable success by substantially shortening the time required for varietal development. Watson et al. [18] reported 4–6 generations per year in wheat, barley, and pea, and approximately four in canola under a 22 h light/2 h dark photoperiod using controlled temperature and light-emitting diode (LED) illumination. Similarly, Ghosh et al. [20] optimized the same photoperiod conditions, achieving up to six generations in wheat and barley, 4–5 in canola, and 4–6 in pea. Notable outcomes include the development of high-protein wheat cultivar 'S Faraday' [21] and disease-resistant barley cultivar 'Scarlett' [22]. However, SB efficacy is more constrained in short-day, photoperiod-sensitive crops such as soybean, where prolonged light can delay flowering through extended accumulation of the active phytochrome form (Pfr) [16].

Advances in controlled-environment lighting—particularly LED systems—have been central to modern SB platforms because they enable precise control of photoperiod, intensity, and spectral composition. LEDs offer high photon efficacy and low radiant heat, supporting tighter canopy-to-light distances and improved space efficiency relative to traditional high-pressure sodium (HPS) systems [7,23,24]. In addition, the spectral output

of LEDs can be tuned to plant physiological requirements [25,26]. By contrast, HPS lamps cannot be spectrally tuned and are relatively deficient in blue wavelengths critical for photosynthesis and morphogenesis [27]. Plants primarily use photosynthetically active radiation (PAR; 400–700 nm) for photosynthesis, where blue light (400–500 nm) serves as a “signal” that regulates chlorophyll synthesis, chloroplast development, and stomatal movements, promoting a shorter, more compact plant architecture [28], and red light (600–700 nm), as the spectral region with the highest quantum efficiency for photosynthesis, constitutes the plant’s primary energy source; it strongly promotes biomass accumulation, starch synthesis, and leaf expansion [29,30]. Beyond PAR, far-red (700–800 nm) can interact with red light via the Emerson Effect [7,31] and can also regulate phytochrome-driven flowering responses and stem elongation through shade-avoidance pathways [30,31]. Consistent with these mechanistic frameworks, broad-spectrum and multi-peak LED recipes have been associated with enhanced photosynthetic efficiency, canopy light penetration, flowering responses, and seed set under controlled systems [32,33].

Although soybean SB research is still emerging, prior studies show that adjusting photoperiod, temperature, and light quality can accelerate flowering and shorten generation time. Jähne et al. [34] reported that a 10 h short-day photoperiod with blue-light-enriched, far-red-depleted LEDs induced flowering within 23 days and maturity within 75–77 days, enabling up to five generations per year in soybean. Nagatoshi and Fujita [35] demonstrated that a 14 h light/10 h dark photoperiod with fluorescent lighting and CO₂ supplementation reduced generation time to ~70 days, enabling up to five generations per year. Lee et al. [36] reported that short-day conditions (9 h light/15 h dark) with optimized LED intensity and controlled temperature and humidity enabled a generation time of ~73 days. In contrast, Aciksoz et al. [37] showed that applying a 22 h long-day photoperiod at flowering, combined with LED lighting and immature seed harvesting, enabled up to six generations per year with high germination rates.

Despite these advances, existing soybean SB protocols disproportionately focus on a narrow set of photoperiods (e.g., 8–10 h, 14 h, or 22 h) [34,35,37–39], and typically employ simplified spectra, leaving intermediate photoperiods (e.g., 18 h) and complex spectral combinations insufficiently characterized. Moreover, while light quality is known to influence flowering time, plant architecture, and pod set, the developmental consequences of varying ratios of high red (HR), deep blue (DB), far-red (FR), cool white (CW), and warm white (WW) wavelengths remain poorly understood in soybean under SB conditions.

To address these gaps, this study evaluated the interactive effects of multiple photoperiod regimes (10, 14, 18, and 22 h light) with four LED spectral combinations characterized by distinct HR, DB, FR, CW, and WW ratios. Seed harvest at different days after sowing (DAS) was further assessed to identify the optimal harvest timing that maximizes seed germination capacity for rapid generation turnover. Finally, plant performance under controlled SB conditions was compared with that of field-grown plants under natural environmental conditions using key traits including days to maturity, biomass, germination rate, pod number, and oil content. Collectively, these results provide practical guidance for optimizing light duration, spectral composition, and harvest timing to accelerate soybean breeding cycles in indoor or semi-controlled breeding pipelines.

2. Materials and Methods

2.1. Plant Material and Experimental Setup

Two registered soybean (*Glycine max* L.) cultivars, ‘Sonya’ and ‘Victoria’, provided by Progen Seed Company (<https://www.progenseed.com>) located in Antakya, Türkiye, were used as plant material. Seeds were untreated (non-coated; no fungicide or insecticide applied) prior to sowing. Although official maturity group (MG) designations are not

reported in the Turkish registration documents, both cultivars were evaluated by the Turkish Seed Registration and Certification Center (TTSM) alongside official MG III–IV standard cultivars during national registration trials. Their flowering performance closely matched those of the MG III–IV standards across multiple testing locations, including Antalya and Adana, providing phenotypic support for their approximate classification as MG III–IV cultivars [40–43]. Because molecular characterization of the major maturity loci (E1–E4 and J) was beyond the scope of this study, the MG designation used throughout the manuscript should be regarded as an approximate phenotypic classification based on official registration trial comparisons.

Growth chamber experiments were conducted in a thermally insulated, steel-framed growth chamber with internal dimensions of 3.61 m (length) $\times$ 1.68 m (width) $\times$ 2.60 m (height). Air temperature was regulated using an air-conditioning unit coupled with heat exchangers, and a humidification device was installed to prevent excessively low relative humidity. All environmental-control devices were integrated into a sensor-based control system operated from an external control panel. Plants were irrigated via a drip irrigation system with timing and duration controlled by a programmable automatic solenoid valve (SMS-TORK Industrial Automation Products, İstanbul, Türkiye). The chamber was subdivided into four compartments using cardboard partitions lined with reflective curtains to minimize light spillover among LED treatments. Each compartment (90 $\times$ 70 $\times$ 90 cm; length $\times$ width $\times$ height) fully encompassed the projected light footprint of its respective LED fixture. Within each photoperiod run, pots were placed in LED-specific compartments with two cultivars ('Sonya' and 'Victoria') arranged as three replicate pots per cultivar per compartment ($n = 3$ pots per cultivar per LED treatment). Pots were positioned directly beneath each LED fixture, and pot positions within each compartment were randomly assigned at the beginning of each experimental run. Photosynthetic photon flux density (PPFD) was periodically verified at the apical canopy level of every plant using a quantum sensor throughout each experimental run, confirming uniform light intensity within each compartment. Periodic PPFD measurements confirmed that no measurable reflection or shading effects occurred within the illuminated area of each compartment. Because all pots remained within the uniformly illuminated area directly beneath the LED fixtures, border effects were considered negligible and were therefore not included as a factor in the statistical analysis. Four LED treatments were employed: GL-A0055, GL-A0056, and GL-A0057 (Fiberli, PSL Electronics, Antalya, Türkiye) [44] and a warm-white LED luminaire (LP300-S, Jupiter Lighting, İstanbul, Türkiye). Treatment configurations remained identical across all photoperiod runs; technical specifications and spectral composition are summarized in Table 1.

2.2. Experimental Design and Growing Conditions

Each photoperiod treatment (22 h, 18 h, 14 h, and 10 h light) was conducted sequentially as a separate temporal block in the same growth chamber. For each run, target air temperature was maintained at 28 ± 2 °C and relative humidity at $\geq 50\%$; photosynthetic photon flux density (PPFD) at canopy height was adjusted to 400–600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ per LED treatment. PPFD was independently verified using a cosine-corrected, full-spectrum quantum sensor (MQ-510; spectral range 389–692 nm; manufacturer-stated calibration uncertainty $< 5\%$), which provides improved measurement accuracy under LED light sources relative to earlier sensor designs; measured values, rather than the manufacturer-declared fixture specifications listed in Table 1, were used as the operational reference for adjusting and reporting light intensity. For the three dimmable Fiberli fixtures (LED-1, GL-A0056; LED-3, GL-A0057; LED-4, GL-A0055), canopy-level PPFD was reduced from the manufacturer-declared maximum to the target range by adjusting the dimmer output

of the integrated control unit, with fixture mounting height kept consistent across compartments (approximately 30–40 cm above the pot rim at the start of each run); for LED-2 (LP300-S; non-dimmable, fixed output), the target PPFD range was achieved by adjusting the vertical distance between the luminaire and the canopy surface, while mounting height was re-verified and corrected as canopy height increased during the experiment. The Fiberli control units do not provide a calibrated percentage of maximum power readout; consequently, exact operating power percentages cannot be reported, and dimmer output was adjusted iteratively against the MQ-510 quantum sensor until the target canopy PPFD of 400–600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ was achieved and verified prior to and during each photoperiod run. Spectral characterization of the three Fiberli horticultural fixtures (GL-A0056, GL-A0057, GL-A0055) was performed by the manufacturer (Fiberli, PSL Electronics, Antalya, Türkiye) using an ASENETEK Lighting Passport ALP-01 spectroradiometer (Asensetek Inc., Hsinchu, Taiwan; spectral range 200–2000 nm) at canopy level, at the fixture-to-canopy distance maintained throughout the experiment. The instrument reports per-channel PPF (photosynthetic photon flux, 400–700 nm, $\mu\text{mol}\cdot\text{s}^{-1}$) and total fixture BPF (blue photon flux, 420–480 nm, integrated across all channels, $\mu\text{mol}\cdot\text{s}^{-1}$) directly from its output table, without assumed spectral fractions. Red:blue (R:B) ratios were calculated as the 660 nm narrow-band channel PPF divided by total fixture BPF (420–480 nm), which integrates blue-region photon flux contributions across all fixture channels emitting within the 420–480 nm range. This definition differs from the conventional broadband R:B formulation (600–700 nm/400–500 nm); however, for these fixtures the 660 nm narrow band channel constitutes the dominant source of red-region photon flux, and the treatment ranking is robust to the choice of integration limits; per-channel PPF values are reported in Table 1. Red:far-red (R:FR) ratios were calculated as the 660 nm channel PPF divided by the 730 nm channel PPF. All Fiberli fixtures employ simultaneous proportional dimming of all LED channels, confirmed in writing by the manufacturer, ensuring that R:B and R:FR ratios remain invariant across dimmer settings and apply directly to the experimental canopy-level PPFD range of 400–600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Per-channel PPF₆₆₀, PPF₇₃₀, and BPF_{420–480} values derived from ASENETEK ALP-01 measurements, together with calculated R:B and R:FR ratios, are reported in Table 1. It should be noted that spectroradiometric measurements were acquired at maximum fixture output rather than at the reduced dimming level applied during the experiment; however, because all LED channels within each fixture are dimmed simultaneously and proportionally under the integrated control unit, the relative spectral composition—and therefore all derived R:B and R:FR ratios—is expected to remain unchanged under the operational canopy-level PPFD conditions. This constitutes a limitation in that operating-condition spectra were not independently verified at every dimming setting, and it is now explicitly acknowledged as such. Plants were grown in 20 cm-diameter × 20 cm-depth pots filled with a 3:2:1 (v/v/v) mixture of field soil (sieved, non-sterilized), peat, and perlite. Within each photoperiod run, pots were placed in LED-specific compartments with two cultivars ('Sonya' and 'Victoria') arranged as three replicate pots per cultivar per compartment (n = 3 pots per cultivar per LED treatment). A total of 6–7 seeds were sown per pot, and seedlings were thinned to one plant per pot at the V2–V3 stage (second or third fully expanded trifoliate leaf stage), prior to the onset of flowering (R1). Irrigation was supplied 2–3 days per week for 3–5 min per event at a drip discharge rate of 40 mL·min^{−1} per pot (120–200 mL per event). A balanced fertilizer solution (18–18–18 + TE) was applied by hand-watering separately from the drip irrigation system, 5–6 times per run, maintaining nutrient-solution electrical conductivity (EC) at 1.5–2.0 mS·cm^{−1} and pH at 6.0–6.5. Before each photoperiod run, the growth chamber was sanitized with 5% commercial bleach followed by Tsunami 100 (15% peracetic acid) and left empty for 24 h. Air temperature, relative humidity, and CO₂ concentration were monitored

throughout each run using integrated control-panel sensors and a Green Eye Desktop CO₂ Logger (model AZ-7798; AZ Instrument Corp., Taichung, Taiwan). The AZ-7798 logger is equipped with a stable nondispersive infrared (NDIR) CO₂ sensor and was operated under the manufacturer's factory calibration; no additional laboratory calibration was performed before the experiment. According to the manufacturer, the instrument provides a CO₂ measurement accuracy of ± 50 ppm $\pm 5\%$ of the measured value and is specified for operation at 5–80% relative humidity under non-condensing conditions. The logger was used to verify the temporal stability of chamber CO₂ concentration throughout the experiment rather than for high-precision gas-exchange measurements.

Table 1. Technical specifications, LED group configuration, and instrument-measured spectral ratios of LED treatments used in this study.

LED Treatments	LED Configuration *	Instrument-Measured Spectral Parameters ***					
		Max. Output PPFD ** ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	R:B	R:FR	PPF ₆₆₀ ($\mu\text{mol}\cdot\text{s}^{-1}$)	PPF ₇₃₀ ($\mu\text{mol}\cdot\text{s}^{-1}$)	BPF _{420–480} ($\mu\text{mol}\cdot\text{s}^{-1}$)
LED-1 (GL-A0056); 600 W; Dimmable	19 groups HR; 5 groups DB; 1 group FR	1200	0.44	57.6	1287.24	22.34	2898.05
LED-2 (LP300-S); 2 × 300 W; Fixed	1 group WW	800	–	–	–	–	–
LED-3 (GL-A0057); 600 W; Dimmable	11 groups HR; 4 groups DB; 2 groups FR; 7 groups CW	1200	0.15	20.5	443.38	21.68	3033.03
LED-4 (GL-A0055); 600 W; Dimmable	16 groups HR; 2 groups DB; 2 groups FR; 4 groups CW	1200	0.62	81.7	1716.32	21.02	2786.00

* A 'group' denotes one independently addressable LED module/channel within the fixture. HR: High Red (640–660 nm); DB: Deep Blue (450–460 nm); FR: Far Red (720–730 nm); WW: Warm White (400–700 nm, 3000 K); CW: Cool White (400–700 nm, 6500 K). GL-A0055, GL-A0056, and GL-A0057 are dedicated horticultural fixtures (Fiberli, PSL Electronics, Antalya, Türkiye). ** PPFD values listed are manufacturer-declared maximum fixture outputs; canopy-level operating PPFD was independently measured using an Apogee MQ-510 quantum sensor (Apogee Instruments, Logan, UT, USA) and adjusted to 400–600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ per treatment prior to and during each photoperiod run (see Section 2.2 for details). *** R:B (red-to-blue ratio) and R:FR (red-to-far-red ratio) derived from Spectroradiometric measurements provided by the manufacturer (Fiberli, PSL Electronics, Antalya, Türkiye) and acquired using an ASESETTEK Lighting Passport ALP-01 (Asensetek Inc., Hsinchu, Taiwan; spectral range 200–2000 nm) at canopy level. R:B = PPF₆₆₀ (660 nm channel, $\mu\text{mol}\cdot\text{s}^{-1}$)/BPF_{420–480} (420–480 nm integrated, $\mu\text{mol}\cdot\text{s}^{-1}$); R:FR = PPF₆₆₀ (660 nm channel)/PPF₇₃₀ (730 nm channel). This R:B definition differs from the conventional broadband formulation (600–700 nm/400–500 nm); however, the 660 nm channel is the dominant red-region source in these fixtures and the treatment ranking (LED-4 > LED-1 > LED-3) is robust to the choice of integration limits; per-channel PPF₆₆₀, PPF₇₃₀, and BPF_{420–480} values derived from manufacturer-provided measurements are reported in Table 1. Under confirmed proportional dimming of all LED channels (manufacturer: PSL Electronics, Antalya, Türkiye), spectral ratios are invariant across dimmer settings and apply directly to the canopy-level PPFD of 400–600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ used during the experiment. ("–": not determined).

The field experiment was conducted at the research farm of Akdeniz University Faculty of Agriculture, Antalya, Türkiye (36°53'59" N, 30°39'05" E). 'Sonya' and 'Victoria' were sown on 31 May 2023 and harvested on 16 October 2023 in separate plots of four rows, each containing 10 plants with 20 cm within-row spacing and approximately 70 cm between-row spacing. Irrigation was provided by drip irrigation according to crop demand; no fertilization was applied, and weeds were controlled manually. For each cultivar, four plants from the central rows were selected for all observations. Over the experimental period, astronomical daylength decreased from 14.50 h (31 May) to 11.12 h (16 October), with a seasonal mean of 13.46 h. The corresponding mean 2 m air temperature and relative humidity were 26.54 °C and 50.29%, respectively, derived from NASA POWER-gridded daily meteorological data [45].

2.3. Measurements and Data Collection

Phenological development was recorded throughout all experiments according to the soybean developmental staging system described by Fehr et al. [46]. Plant height was

measured from the substrate or soil surface to the apical meristem at each observation date; the maximum value recorded throughout the trial period for each plant was used as the response variable in subsequent analyses.

For aboveground biomass determination, each plant was removed from its pot and separated at the root–shoot junction. Shoot tissues (stems and leaves) were oven-dried at 45 °C for 5 days; drying was considered complete when two consecutive dry-weight measurements were identical, after which the final dry weight was recorded. From the full seed (R6) stage onward, pods were collected via serial harvests to obtain seeds at different developmental stages. Immature seeds were dried within intact pods at 37 °C for 24 h following the post-harvest drying procedure described by Jähne et al. [34] before germination testing. After drying, seeds were kept at 4 °C for approximately 24 h prior to sowing as part of a standardized post-harvest handling procedure. Seeds were subsequently sown in seedling trays filled with peat and covered with a thin layer of perlite, and trays were maintained at 28 °C in darkness until emergence (approximately 3–4 days). After emergence, trays were transferred to Venlo-type greenhouses and maintained under standard greenhouse conditions. Seedling emergence, used as a proxy for germination capacity, was assessed 10 days after sowing by counting the number of seedlings that had emerged above the growing medium surface. Throughout this manuscript, germination refers to this emergence-based assessment under controlled germination conditions.

Following harvest at the R8 (full maturity) stage, seeds were collected for laboratory determination of total seed oil concentration and fatty acid composition. For oil analyses, the experimental unit (biological replicate) consisted of one pooled seed lot harvested from a single plant. Under controlled-environment conditions, each replicate was obtained from one pot-grown plant, whereas in the field experiment each replicate was obtained from one individually sampled field-grown plant. Individual seeds within each seed lot were not treated as independent observations. Fatty-acid composition and total seed oil concentration (%) were determined for myristic, palmitic, stearic, oleic, linoleic, linolenic, arachidic, 11-eicosenoic, behenic, and lignoceric acids.

2.4. Statistical Analysis

All analyses were conducted in R (v.4.5.2) [47] using the following packages: lme4 (v.1.1-38) for linear mixed-effects models [48], glmmTMB (v.1.1-13) for generalized linear-mixed models [49], emmeans (v.2.0.2) for estimated marginal means and Tukey-adjusted pairwise comparisons [50], and vegan (v.2.7-2) for multivariate analyses (PERMANOVA and CLR-PCA) [51]. Figures were generated using ggplot2 (v.4.0.2) [52].

Analyses were performed at the plant level using model structures that reflected the experimental design and hierarchical clustering. In the growth-chamber experiment, the photoperiod × LED-specific compartment combination represented the experimental unit, with individual plants serving as subsamples. Random intercepts were specified for each experimental unit to account for within-compartment non-independence. Because photoperiod treatments were conducted as sequential runs, photoperiod effects were inherently confounded with temporal variation. The mixed-model random effects accounted for hierarchical dependence within runs but did not eliminate this confounding.

Statistical models were selected a priori based on experimental design and response variable distributions. Developmental timing (days to R1 and R6) was analyzed using linear mixed-effects models with environment (10 h, 14 h, 18 h, 22 h, and field), cultivar, and their interaction as fixed effects. Secondary analyses within each photoperiod included LED treatment, cultivar, and their interaction as fixed effects, with denominator degrees of freedom estimated using the Satterthwaite approximation. Stem dry weight was analyzed after logarithmic transformation using linear mixed-effects models. Pod number

was analyzed using negative binomial generalized linear mixed models to account for overdispersion. Germination proportions were analyzed using beta-binomial generalized linear mixed models due to extra-binomial variation among units.

Total seed oil concentration was examined through two complementary linear models. The environment comparison included 10 h and 14 h photoperiods and the field experiment, with environment, cultivar, and their interaction as fixed effects. A separate LED-only analysis included all controlled-environment samples with photoperiod, cultivar, LED treatment, and the photoperiod $\times$ cultivar interaction as fixed effects. Fatty acid composition was analyzed as compositional data following centered log-ratio (CLR) transformation, with multivariate differences evaluated by PERMANOVA and visualized by CLR-PCA.

Estimated marginal means were compared using Tukey-adjusted pairwise comparisons ($\alpha = 0.05$). Due to the balanced design, similar standard errors across treatment levels reflect the expected precision of the fitted mixed-effects models rather than identical variability in raw observations.

3. Results

3.1. Environmental Conditions and Trial Duration

Mean air temperature, relative humidity, CO₂ concentration, and trial duration for each controlled-environment photoperiod treatment, together with field-derived temperature and humidity data (NASA POWER), are summarized in Table 2. Growth-chamber runs were maintained close to the target temperature range (27.6–28.8 °C) with mean RH of 57.8–65.7% and mean CO₂ of 524–587 ppm. The field period (31 May–16 October 2023) had a mean 2 m air temperature (T2M) of 26.5 °C and mean 2 m relative humidity (RH2M) of 50.3% (Table 2). Atmospheric CO₂ concentration was not measured in the field; the ambient outdoor CO₂ at the experimental site during the trial period was approximately 420 ppm (global mean), which is approximately 100–170 ppm lower than the CO₂ levels recorded in the growth chamber (524–587 ppm). This difference may have contributed to contrasts in photosynthetic rate and biomass between environments.

Table 2. Mean environmental conditions and trial duration for controlled-environment photoperiod trials and the field period.

Environment	Mean Air Temperature (°C)	Mean Relative Humidity (%)	Mean CO ₂ (ppm)	Trial Duration (Day)	DLI ** (mol·m ⁻² ·day ⁻¹)
22 h	27.6	60.3	580	88	39.6
18 h	27.9	57.8	524	131	32.4
14 h	28.3	61.6	556	89	25.2
10 h	28.8	65.7	587	88	18.0
Field (mean daylength = 13.46 h)	26.5 *	50.3 *	-	138	-

* Data derived from NASA POWER Project, 2026 [45]. ** Daily light integral (DLI; mol·m⁻²·day⁻¹) was calculated as $DLI = PPFD \times photoperiod (h) \times 3600/10^6$, using a midpoint PPFD of 500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, representing the center of the 400–600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ target range maintained uniformly across all LED treatments within each photoperiod. Because canopy PPFD was equalized across LED treatments within each photoperiod run, DLI did not differ among LED treatments and did not confound spectral comparisons. DLI is not reported for the field environment as solar irradiance was not continuously measured during the trial period. (“-”: not determined).

3.2. Developmental Timing

Developmental timing was evaluated using a two-stage analytical framework. First, an overall mixed-effects analysis estimated the effects of environment (photoperiod treatments plus the field environment) and cultivar. Second, photoperiod-specific analyses were performed using growth-chamber data to determine whether developmental timing differed among individual LED compartments within each photoperiod. Across both cultivars, plants grown under the 22 h photoperiod did not reach R6, and under the 18 h

photoperiod, the LED-3 treatment also failed to reach R6; therefore, R6 comparisons are restricted to environments where R6 was observed. Type III mixed-model ANOVA indicated a strong environment effect (encompassing photoperiod treatments and the field trial) on both developmental stages, whereas cultivar and the environment $\times$ cultivar interaction were not significant (Table S1). The environment effect was highly significant for R1 ($F_{4,30} = 150.3$, $p < 0.0001$) and R6 ($F_{3,22} = 536.1$, $p < 0.0001$), whereas cultivar was non-significant for R1 ($p = 0.3342$) and R6 ($p = 0.6505$) and the environment $\times$ cultivar interaction was similarly non-significant ($p \geq 0.2622$) (Table S1). Model-adjusted means (LSMeans $\pm$ SE) and 95% confidence intervals for days after sowing (DAS) to R1 and R6 are presented in Table 3.

Table 3. Model-adjusted means (LSMeans $\pm$ SE) for DAS to R1 and R6 across environments and cultivars.

Environment	Cultivar	R1 Stage		R6 Stage	
		DAS (LSMean $\pm$ SE)	95% CI	DAS (LSMean $\pm$ SE)	95% CI
10 h	‘Sonya’	24.5 $\pm$ 1.96	20.5–28.5	50.0 $\pm$ 1.87	46.1–53.9
10 h	‘Victoria’	24.5 $\pm$ 1.96	20.5–28.5	50.2 $\pm$ 1.87	46.3–54.1
14 h	‘Sonya’	27.1 $\pm$ 1.96	23.2–31.2	56.5 $\pm$ 1.87	52.6–60.4
14 h	‘Victoria’	27.0 $\pm$ 1.96	23.0–31.0	59.7 $\pm$ 1.87	55.8–63.6
18 h	‘Sonya’	68.2 $\pm$ 1.96	64.2–72.2	124.5 $\pm$ 2.16	120.0–129.0
18 h	‘Victoria’	63.0 $\pm$ 1.96	59.0–67.0	119.4 $\pm$ 2.16	114.9–123.9
22 h	‘Sonya’	28.0 $\pm$ 1.96	24.0–32.0	-	-
22 h	‘Victoria’	28.0 $\pm$ 1.96	24.0–32.0	-	-
Field	‘Sonya’	36.0 $\pm$ 1.96	32.0–40.0	92.5 $\pm$ 1.87	88.6–96.4
Field	‘Victoria’	35.3 $\pm$ 1.96	31.3–39.25	91.7 $\pm$ 1.87	87.9–95.6

LSMeans are model-based estimated marginal means; therefore, their standard errors reflect the fitted mixed-effects model rather than the variability of the raw observations. Similar SE values across environments are expected under the balanced experimental design.

Tukey-adjusted contrasts showed that the 10 h and 14 h photoperiods accelerated R1 by approximately 9–12 d relative to the field in both cultivars ($p \leq 0.042$), whereas the 18 h photoperiod markedly delayed R1 by approximately 28–32 d compared with the field ($p < 0.0001$). Differences between 10 h and 14 h were not significant for R1 (Tables 3 and S2). For R6, the 10 h and 14 h photoperiods accelerated development by approximately 32–43 d relative to the field ($p \leq 0.0001$), whereas the 18 h photoperiod delayed R6 by approximately 28–32 d relative to the field and by approximately 60–75 d relative to 10 h and 14 h ($p < 0.0001$) (Tables 3 and S3). The 10 h vs. 14 h difference for R6 was not significant in ‘Sonya’ but was significant in ‘Victoria’, indicating slightly faster progression under 10 h in that cultivar.

To determine whether individual LED compartments contributed measurable variation in developmental timing beyond the overall photoperiod effect, R1 and R6 were further analyzed using photoperiod-specific mixed models and LED treatment-specific comparisons (Table S4). For R1, Type III ANOVA showed a highly significant photoperiod effect ($p < 0.0001$), whereas LED treatment, cultivar, and the photoperiod $\times$ cultivar interaction were not significant ($p \geq 0.512$). Photoperiod-specific LS-means indicated the earliest R1 under 10 h (~24 DAS) and 14 h (~27 DAS), intermediate timing under 22 h (~28 DAS), and a strong delay under 18 h (~63–70 DAS). Within each photoperiod, all LED treatments received identical CLD groupings, indicating negligible spectral effects on R1 (Table S5). Photoperiod effects on R6 were even more pronounced ($p < 0.0001$), while LED treatment, cultivar, and the photoperiod $\times$ cultivar interaction were not significant ($p \geq 0.190$). LS-means indicated the fastest progression to R6 under 10 h (~48–51 DAS),

followed by 14 h (~56–59 DAS), and substantially later under 18 h (~120–123 DAS); the 22 h regime was excluded from R6 analysis as that stage was never reached. LED treatments were not significantly different within any photoperiod for R6 (identical CLD groupings; Table S6). Taken together, photoperiod was the dominant determinant of developmental timing, with the 10 h regime providing the most rapid seed-to-seed progression among the evaluated conditions. LS-means ($\pm$ SE) for DAS to R1 and R6 within each photoperiod and LED combination are presented in Figure 1.

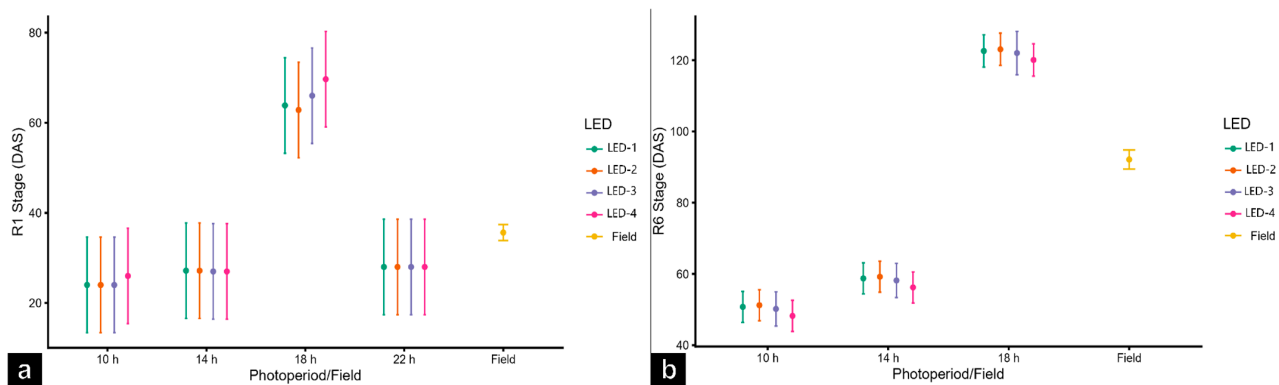


Figure 1. Estimated marginal means (EMMs) and 95% confidence intervals for soybean developmental stages R1 and R6 (days after sowing) derived from linear mixed-effects models. Each point represents the model-estimated mean for an environment $\times$ LED treatment combination, averaged across cultivars ('Sonya' and 'Victoria'). (a) R1 stage at 10 h, 14 h, 18 h, 22 h, and field photoperiods for LED-1, LED-2, LED-3, and LED-4. (b) R6 stage at 10 h, 14 h, 18 h, and field photoperiods for LED-1, LED-2, LED-3, and LED-4. Plants under the 22 h photoperiod did not reach the R6 stage.

3.3. Plant Height

Maximum plant height differed significantly among environments and between cultivars. Type III ANOVA indicated significant effects of environment ($F_{4,93} = 21.40$, $p < 0.0001$) and cultivar ($F_{1,93} = 7.86$, $p = 0.0061$), as well as a significant environment $\times$ cultivar interaction ($F_{4,93} = 3.18$, $p = 0.0170$), indicating that cultivar differences in height were dependent on the environment (Table S7). Estimated marginal means (EMMs) were greatest under the 18 h photoperiod (122.8 cm) and lowest under 22 h (80.7 cm), whereas the field mean (96.6 cm) was comparable to those observed under 10 h (96.3 cm) and 14 h (91.7 cm) (Table 4; Figure 2a).

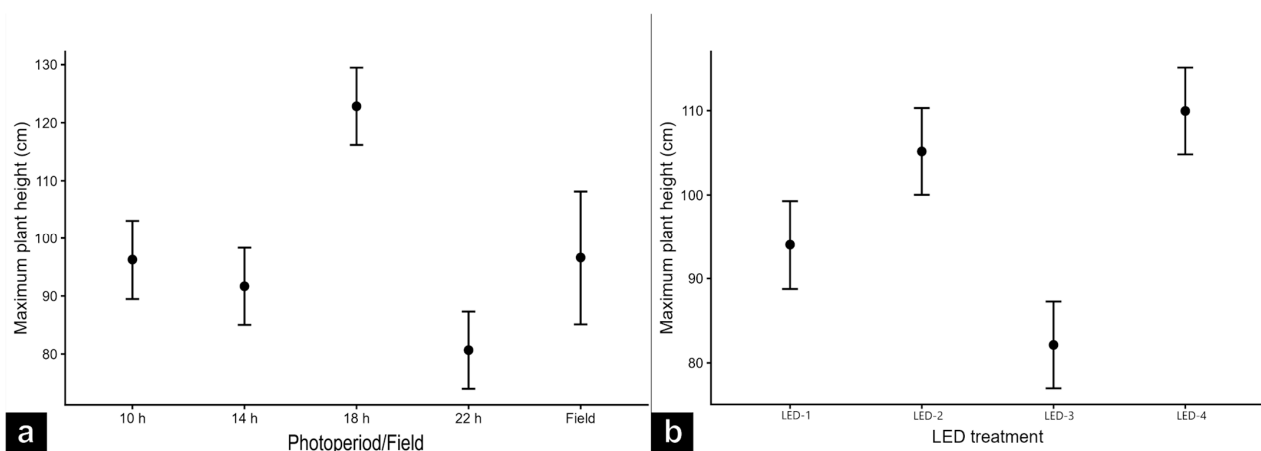


Figure 2. Estimated marginal means of maximum plant height, error bars indicate 95% confidence intervals: (a) for photoperiod treatments (10 h, 14 h, 18 h, 22 h) and field trial, marginal over cultivar. (b) for LED treatments (LED-1, LED-2, LED-3, LED-4) marginal over cultivar.

Table 4. Estimated marginal means (EMMs) for maximum plant height across environments and cultivars.

Effect	Environment	Cultivar	EMM (cm)	SE	df2 *	95% CI (Lower)
Environment (marginal)	10 h	Both	96.27	3.43	93	89.47–103.08
Environment (marginal)	14 h	Both	91.67	3.35	93	85.01–98.32
Environment (marginal)	18 h	Both	122.83	3.35	93	116.18–129.49
Environment (marginal)	22 h	Both	80.67	3.35	93	74.01–87.32
Environment (marginal)	Field	Both	96.62	5.8	93	85.10–108.15
Environment within cultivar	10 h	‘Sonya’	109.00	4.74	93	99.59–118.41
Environment within cultivar	14 h	‘Sonya’	103.67	4.74	93	94.26–113.08
Environment within cultivar	18 h	‘Sonya’	125.67	4.74	93	116.26–135.08
Environment within cultivar	22 h	‘Sonya’	82.42	4.74	93	73.01–91.83
Environment within cultivar	Field	‘Sonya’	92.25	8.21	93	75.95–108.55
Environment within cultivar	10 h	‘Victoria’	83.55	4.95	93	73.72–93.37
Environment within cultivar	14 h	‘Victoria’	79.67	4.74	93	70.26–89.08
Environment within cultivar	18 h	‘Victoria’	120.00	4.74	93	110.59–129.41
Environment within cultivar	22 h	‘Victoria’	78.92	4.74	93	69.51–88.33
Environment within cultivar	Field	‘Victoria’	101.00	8.21	93	84.70–117.30

* EMM, Estimated marginal means, df2: denominator degrees of freedom, SE: Standard error.

Within the growth chamber, maximum plant height was significantly affected by photoperiod ($F_{3,84} = 47.91, p < 0.0001$), cultivar ($F_{1,84} = 32.14, p < 0.0001$), and LED treatment ($F_{3,84} = 23.02, p < 0.0001$), with a significant photoperiod $\times$ cultivar interaction ($F_{3,84} = 5.13, p = 0.0026$) (Table S8). Tukey-adjusted comparisons showed that LED-3 produced the shortest plants (82.1 cm; CLD group a), followed by LED-1 (94.0 cm; CLD group b), whereas LED-2 and LED-4 were not significantly different from each other (105–109 cm; CLD group c) (Tables S9 and S10; Figure 2b).

3.4. Stem Dry Weight

Stem dry weight differed strongly among environments. Type III tests revealed a significant environment effect ($F_{4,15.72} = 188.46, p < 0.0001$) and a significant cultivar effect ($F_{1,79.78} = 10.96, p = 0.0014$), whereas the environment $\times$ cultivar interaction was not significant ($p = 0.418$), indicating broadly consistent cultivar differences across environments (Table S11). Model-adjusted means indicated the lowest stem dry weight under 10 h and 14 h, progressively greater values under 18 h and 22 h, and the greatest dry weight in field-grown plants for both cultivars (Table 5; Figure 3a).

Table 5. Model-adjusted means for stem dry weight across environments and cultivars.

Environment	Cultivar	LSMean $\pm$ SE (g)	95% CI
10 h	‘Sonya’	3.22 $\pm$ 0.30	2.47–4.19
14 h	‘Sonya’	5.13 $\pm$ 0.47	3.94–6.68
18 h	‘Sonya’	31.09 $\pm$ 2.86	23.88–40.49
22 h	‘Sonya’	16.14 $\pm$ 1.49	12.39–21.01
Field	‘Sonya’	70.10 $\pm$ 7.95	51.59–95.24
10 h	‘Victoria’	3.06 $\pm$ 0.28	2.35–3.99
14 h	‘Victoria’	4.51 $\pm$ 0.42	3.46–5.87
18 h	‘Victoria’	27.56 $\pm$ 2.54	21.17–35.89
22 h	‘Victoria’	15.73 $\pm$ 1.45	12.08–20.49
Field	‘Victoria’	54.30 $\pm$ 6.16	39.97–73.78

Within the growth chamber, stem dry weight was significantly affected by photoperiod ($F_{3,16} = 389.39, p < 0.0001$), cultivar ($F_{1,80} = 6.12, p = 0.0155$), and LED treatment ($F_{3,16} = 6.60,$

$p = 0.0041$), with no significant photoperiod $\times$ cultivar interaction ($p = 0.603$) (Table S12). LED treatment-level EMMs showed the highest stem dry weight under LED-4 and the lowest under LED-2, with LED-1 and LED-3 occupying intermediate positions (Table S13; Figure 3b).

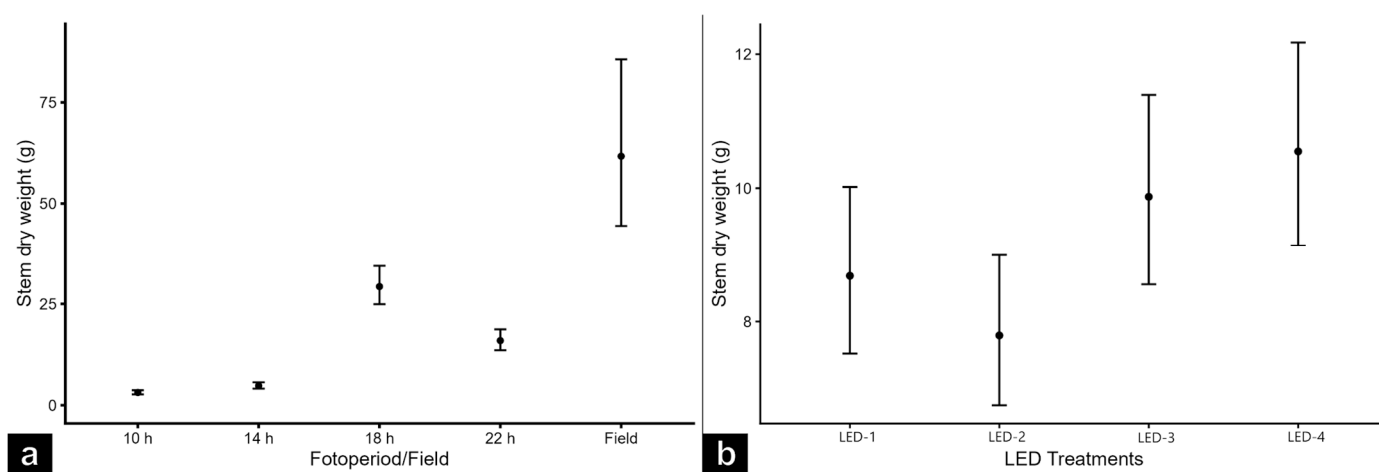


Figure 3. Estimated marginal means of stem dry weight (g), error bars indicate 95% confidence intervals: (a) for photoperiod treatments (10 h, 14 h, 18 h, 22 h) and field trial, marginal over cultivar. (b) for LED treatments (LED-1, LED-2, LED-3, LED-4) marginal over cultivar.

3.5. Pod Number

Pod numbers, assessed on plants reaching R6 or later, differed among environments and between cultivars. Type III tests indicated significant effects of environment ($p < 0.0001$) and cultivar ($p = 0.014$), with a significant environment $\times$ cultivar interaction ($p = 0.030$) (Table S14), indicating that the magnitude of cultivar differences in pod set depended on the growing environment. Pod production under LED photoperiods was substantially lower than in the field for both cultivars ('Sonya': 234.4 ± 73.8 pods.plant⁻¹; 'Victoria': 280.3 ± 88.2 pods.plant⁻¹). Within LED-controlled conditions, pod number was moderate under 10 h ('Sonya': 22.6 ± 6.9 ; 'Victoria': 16.2 ± 5.0) and 14 h ('Sonya': 29.9 ± 9.0 ; 'Victoria': 26.4 ± 8.0), but low under 18 h ('Sonya': 4.38 ± 1.51 ; 'Victoria': 6.11 ± 2.06) (Table 6; Figure 4a). The substantially reduced pod number under 18 h is consistent with delayed progression to R6 under this photoperiod and with the absence of harvestable pods in the LED-3 treatment within the 18 h run. The 22 h photoperiod was excluded from pod number analysis as R6 was not attained. Within photoperiods, LED treatment identity did not exert a detectable effect on pod number (Table S15; Figure 4b).

Table 6. Model-adjusted means and CLD groupings for pod number across environments and cultivars.

Environment	Cultivar	LSMean $\pm$ SE (pods.plant ⁻¹)	95% CI	CLD *
18 h	'Sonya'	4.38 ± 1.51	1.86–10.31	a
10 h	'Sonya'	22.59 ± 6.86	10.60–48.15	b
14 h	'Sonya'	29.88 ± 9.03	14.07–63.46	b
Field	'Sonya'	234.42 ± 73.79	107.02–513.46	c
18 h	'Victoria'	6.11 ± 2.06	2.64–14.17	a
10 h	'Victoria'	16.20 ± 4.96	7.56–34.73	ab
14 h	'Victoria'	26.44 ± 8.01	12.43–56.23	b
Field	'Victoria'	280.33 ± 88.16	128.08–613.57	c

* Letters indicate compact letter display (CLD) from Tukey-adjusted pairwise comparisons. Means sharing at least one letter are not significantly different ($p < 0.05$).

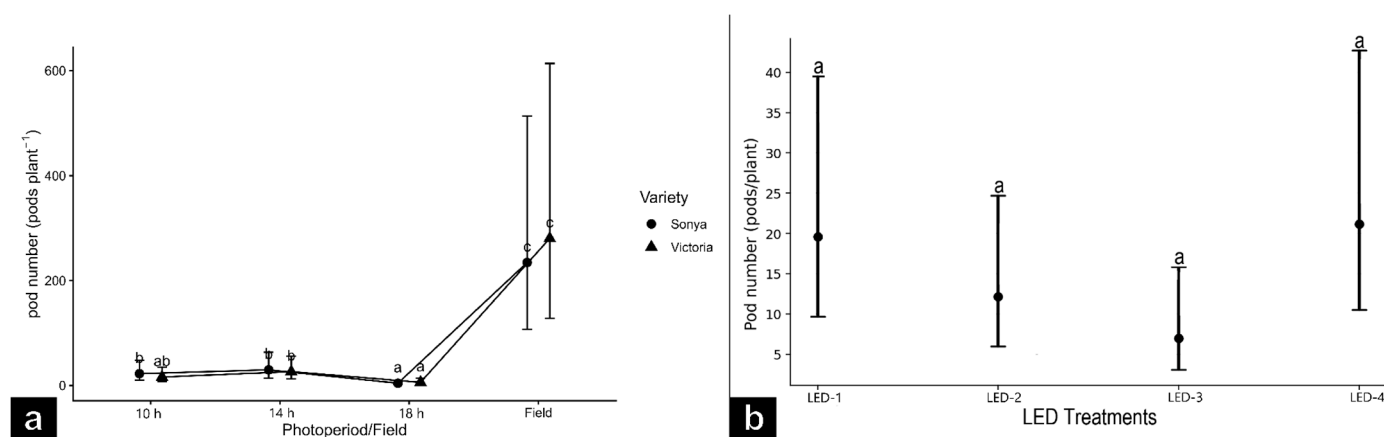


Figure 4. Estimated marginal means of pod number (pods.plant⁻¹), error bars indicate 95% confidence intervals: (a) for photoperiod treatments (10 h, 14 h, 18 h, 22 h) and field trial, marginal over cultivar; (b) for LED treatments (LED-1, LED-2, LED-3, LED-4) marginal over cultivar. Letters indicate compact letter display (CLD) from Tukey-adjusted pairwise comparisons. Means sharing at least one letter are not significantly different ($p < 0.05$).

3.6. Seed Oil Concentration and Fatty-Acid Composition

Total seed oil concentration and fatty acid composition were analyzed using seeds harvested at the R8 stage from the 10 h, 14 h, and field environments; the 18 h and 22 h treatments were excluded as plants did not reach R8 under those conditions. Biological replicates were defined as one pooled seed lot harvested from a single experimental pot. Under controlled-environment conditions, each photoperiod included four independent LED compartments, each providing two biological replicates per cultivar. The field experiment yielded two biological replicates per cultivar. The environment comparison was thus based on 36 biological observations, while the LED-only analysis comprised 32 biological observations.

Total seed oil concentration was significantly affected by environment ($F_{2,30} = 5.96$, $p = 0.0066$) and cultivar ($F_{1,30} = 61.39$, $p < 0.0001$), whereas the environment $\times$ cultivar interaction was not significant ($p = 0.761$) (Table S16). Across genotypes, field-grown plants exhibited the highest oil concentration (20.67%), followed by 10 h (19.44%) and 14 h (18.35%). ‘Sonya’ consistently showed higher oil content than ‘Victoria’ in all environments, and the non-significant interaction indicated that genotypic differences in oil accumulation were stable across environmental conditions (Table 7; Figure 5a). Within the growth chamber, total seed oil concentration was significantly affected by photoperiod ($F_{1,25} = 9.53$, $p = 0.0049$), cultivar ($F_{1,25} = 122.16$, $p < 0.0001$), and LED treatment ($F_{3,25} = 9.08$, $p = 0.0003$), while the photoperiod $\times$ cultivar interaction was not significant (Table S17). EMMs indicated higher oil concentration under 10 h relative to 14 h, a consistent ‘Sonya’ advantage over ‘Victoria’, and LED-3 producing the highest oil concentration among LED treatments (Table 8; Figure 5b).

Table 7. Estimated marginal means (EMMs) for total seed oil concentration across environments and cultivars.

Environment	Cultivar	EMM (%)	95% CI
10 h	‘Sonya’	21.32	20.37–22.27
10 h	‘Victoria’	17.56	16.60–18.51
14 h	‘Sonya’	20.37	19.42–21.33
14 h	‘Victoria’	16.32	15.37–17.28
Field	‘Sonya’	23.1	21.19–25.01
Field	‘Victoria’	18.24	16.34–20.15

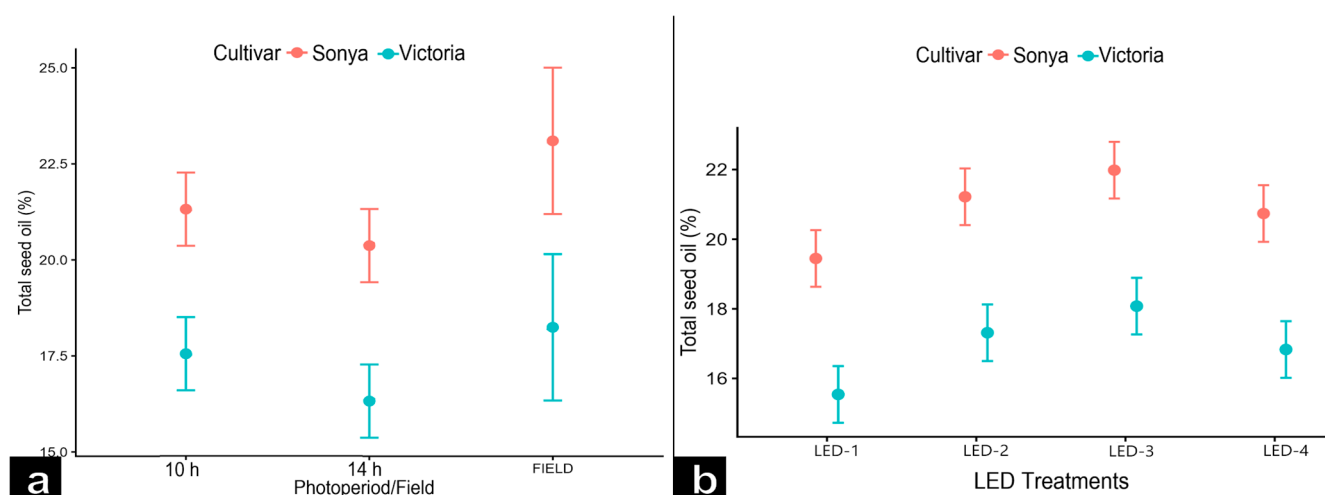


Figure 5. Estimated marginal means of total seed oil (%), error bars indicate 95% confidence intervals: (a) for photoperiod treatments (10 h, 14 h) and field trial, across cultivar; (b) for LED treatments (LED-1, LED-2, LED-3, LED-4) across cultivar.

Table 8. Estimated marginal means (EMMs) for total seed oil concentration by LED treatment (marginal over photoperiod and cultivar).

LED Treatment	EMM (%)	95% CI
LED-1	17.5	16.77–18.22
LED-2	19.3	18.54–19.99
LED-3	20.0	19.30–20.76
LED-4	18.8	18.06–19.51

PERMANOVA analysis of centered log-ratio (CLR)-transformed fatty acid profiles revealed significant multivariate effects of both environment ($F = 12.61$, $R^2 = 0.373$, $p = 0.001$) and cultivar ($F = 10.22$, $R^2 = 0.151$, $p = 0.001$) on fatty acid composition (Table S18). In contrast, the environment $\times$ cultivar interaction was not significant ($F = 1.11$, $R^2 = 0.033$, $p = 0.315$), indicating that genotypic responses to environmental conditions were largely parallel across environments. Environment explained 37.3% of the total compositional variance, whereas cultivar accounted for 15.1%, demonstrating that both cultivation conditions and genotype substantially influenced lipid compositional structure. These findings indicate that fatty acid profiles were environmentally responsive, although the relative environmental response patterns remained stable between cultivars. CLR-PCA of samples from the 10 h, 14 h, and field environments explained 51.8% and 19.4% of the total variance on PC1 and PC2, respectively. Samples from the 10 h and 14 h photoperiods overlapped extensively in PCA space (Figure 6a), whereas field-grown samples showed a distinct displacement along the positive PC1 axis with broader dispersion, suggesting that field cultivation introduced additional variability in seed lipid composition. Varietal separation between ‘Sonya’ and ‘Victoria’ was minimal, indicating that environmental conditions exerted a stronger influence on fatty acid composition than genotypic differences for the cultivars studied.

Restricting the multivariate analysis to growth-chamber samples only, PERMANOVA revealed no significant effect of photoperiod treatment on CLR-transformed fatty acid composition ($F = 1.41$, $R^2 = 0.036$, $p = 0.231$). Likewise, neither the LED treatment ($F = 1.06$, $R^2 = 0.080$, $p = 0.402$) nor the photoperiod $\times$ cultivar interaction ($F = 0.53$, $R^2 = 0.013$, $p = 0.716$) was significant. In contrast, cultivar identity exerted a significant multivariate effect on fatty acid composition ($F = 9.47$, $R^2 = 0.239$, $p = 0.001$), indicating stable

genotype-specific differences in lipid composition across LED treatments. Residual variation accounted for 63.2% of the unexplained compositional variance (Table S19). CLR-PCA of LED treatment samples explained 36.4% (PC1) and 30.6% (PC2) of total compositional variance; confidence ellipses for LED-1 through LED-4 overlapped substantially, indicating that lipid profiles were largely consistent across LED treatments (Figure 6b). Loading analysis indicated that lignoceric and eicosenoic acids contributed positively to PC1, while linolenic and palmitic acids contributed negatively; PC2 was positively influenced by stearic and arachidic acids and negatively by oleic and eicosenoic acids. Hierarchical clustering of CLR-transformed profiles in the heatmap further confirmed the overall similarity of fatty acid compositions across LED photoperiod treatments and field conditions (Figure 7). Collectively, these findings support a pattern in which LED spectral treatment influenced total oil accumulation without inducing systematic shifts in fatty acid proportional composition.

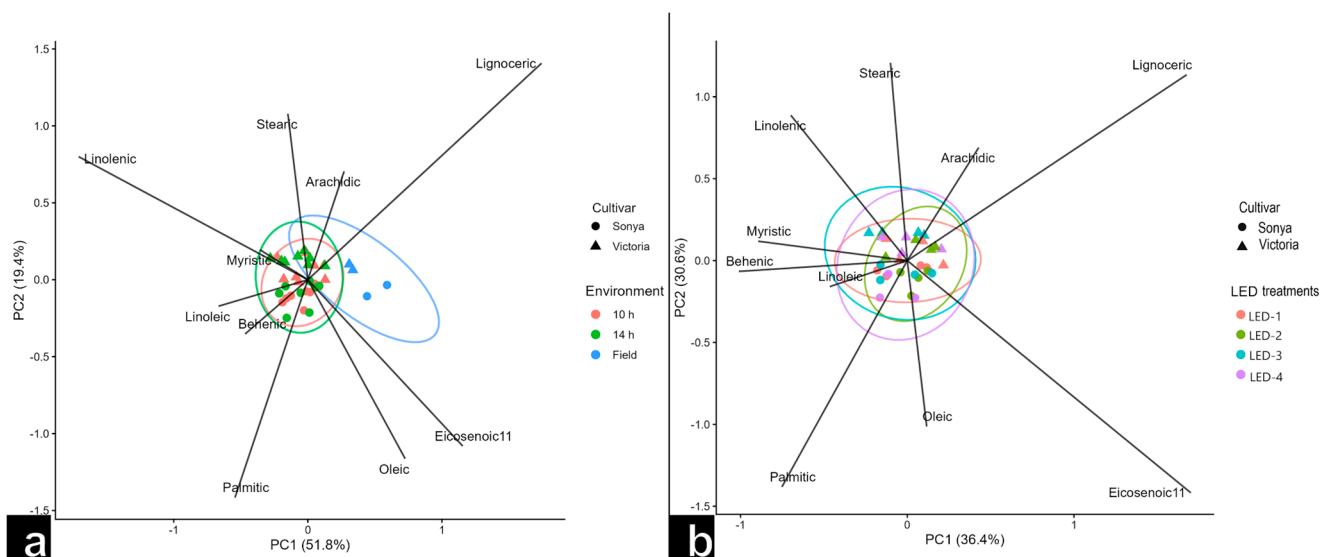


Figure 6. Principal component analysis (PCA) of centered log-ratio (CLR) transformed fatty acid composition. Points represent individual samples colored according to environment/LED treatments and shaped according to cultivar. Ellipses represent multivariate dispersion of samples within each environment/LED treatments. Lines indicate fatty acid loadings contributing to the PCA axes; (a) PCA of CLR-transformed fatty acid composition of soybean seeds across environments (10 h, 14 h photoperiods and field trial); (b) PCA of CLR-transformed fatty acid composition of soybean seeds grown under controlled LED treatments (LED-1, LED-2, LED-3, LED-4).

3.7. Seed Germination

The primary germination analysis was performed using the complete dataset across all eligible harvests (R6–R8), whereas fixed-day DAS analyses were conducted separately only as Supplementary analyses to examine maturity-specific responses.

Germination (emergence) surveys were conducted using seeds produced under LED-controlled conditions from photoperiod treatments that reached R6 or later. Serial pod harvests began at R6 and continued at multiple subsequent DAS. Germination analyses were restricted to seeds obtained under the 10 h and 14 h photoperiods, which were the only LED regimes that consistently produced sufficient healthy seed lots for testing; seeds from the 18 h and 22 h photoperiods (insufficient seed number) and from the field trial were excluded.

Across all eligible harvests (R6–R8), after adjusting for harvest timing and maturity, LED treatment identity significantly affected germination ($\chi^2 = 13.2$, $df = 3$, $p = 0.00430$), indicating treatment-level differences in germination performance after controlling for photoperiod group, cultivar, and harvest covariates (Table S20). Harvest timing variables were also influential (Harvest_DAS: $\chi^2 = 93.9$, $df = 1$, $p = 3.37 \times 10^{-22}$; Harvest_Stage:

$\chi^2 = 6.98$, $df = 2$, $p = 0.0305$), whereas photoperiod and cultivar were not significant in this subset ($p \geq 0.177$) and the photoperiod $\times$ cultivar interaction was negligible ($p = 0.945$). Model-adjusted EMMs indicated the highest germination rates under LED-3 (54.0%; 95% CI: 46.3–61.5; CLD group a) and the lowest under LED-4 (37.8%; 95% CI: 30.4–45.8; CLD group b), with LED-1 (45.6%) and LED-2 (48.9%) occupying intermediate positions (both CLD group ab) (Table 9).

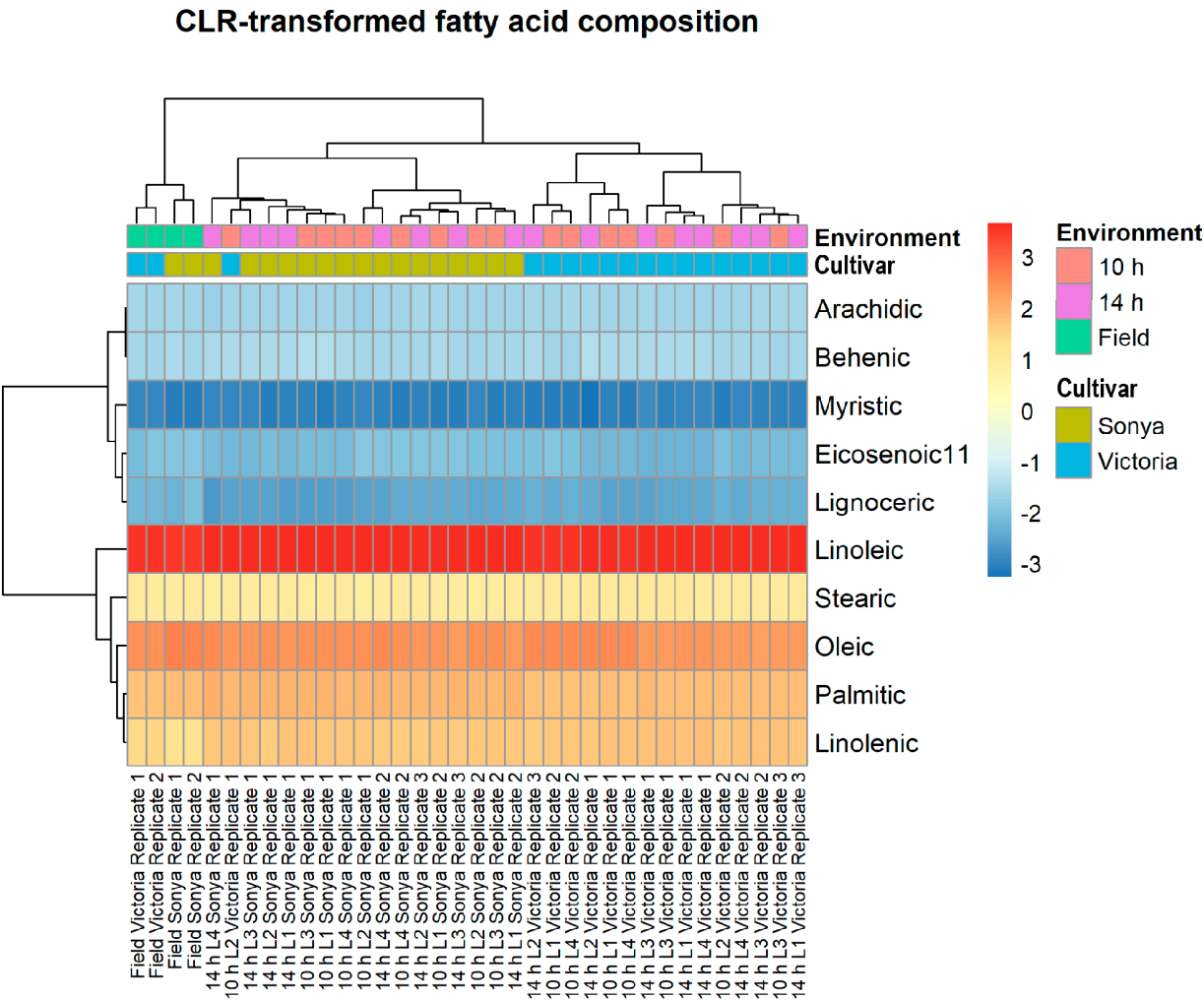


Figure 7. Heatmap of centered log-ratio (CLR) transformed fatty acid composition of soybean seeds grown under controlled LED photoperiod treatments (10 h and 14 h) and field trial. Rows represent fatty acids and columns represent individual samples. Hierarchical clustering was performed using Ward’s method based on Euclidean distance. Annotation bars indicate environments (10 h, 14 h photoperiods, and field trial) and cultivar. Color scale represents relative abundance after CLR transformation, with warmer colors indicating higher relative values and cooler colors indicating lower relative values. The clustering pattern indicates substantial similarity among LED treatments, while field samples show slightly greater dispersion in fatty acid composition.

Table 9. Model-adjusted means (EMMs) and CLD groupings for germination (%) by LED treatment.

LED Treatment	EMM (%)	95% CI	CLD *
LED-3	54.0	46.3–61.5	a
LED-2	48.9	40.8–57.1	ab
LED-1	45.6	38.5–52.8	ab
LED-4	37.8	30.4–45.8	b

* Letters indicate compact letter display (CLD) from Tukey-adjusted pairwise comparisons. Means sharing at least one letter are not significantly different ($p < 0.05$).

To interpret germination differences at comparable maturity windows within each photoperiod, additional fixed-day DAS analyses were conducted using harvest snapshots aligned to R6, R6 + 5, R6 + 10, R6 + 20 (± 1 d), and R8 for the 10 h and 14 h treatments. Germination increased markedly with later harvest timing under both photoperiods, rising from low values near R6 to high values near R8 (Table 10). Using fixed-day DAS binomial GLMs within each photoperiod group, LED treatment effects were not detected at early- and mid-harvest snapshots (R6 through R6 + 20) for either 10 h or 14 h ($p \geq 0.518$ and $p \geq 0.529$, respectively; Table S21), with all LED treatments sharing the same Tukey CLD group at those time points (Table S23). At 10 h, DAS 86, the LED treatment term was significant ($\chi^2 = 27.56$, $df = 3$, $p = 4.49 \times 10^{-6}$); however, three LED treatments reached near-complete germination ($\sim 100\%$), indicating a boundary condition in which inference was driven by a single treatment (LED-4) lagging behind a saturated background rather than reflecting consistent separation across all LED treatments. Cultivar effects and LED treatment $\times$ cultivar interactions were not consistently supported across fixed-day DAS snapshots, with an isolated cultivar signal observed at 10 h DAS 86 ($p = 0.0130$) under the same saturation condition (Table S21).

Table 10. Sample size and observed germination at each harvest DAS within the photoperiod.

Photoperiod	Target (± 1 Day)	DAS	Seeds Tested (n)	Germinated (n)	Observed Germination (%)
10 h	R6	50	152	11	7.24
10 h	R6 + 5	55	111	16	14.41
10 h	R6 + 10	60	100	22	22
10 h	R6 + 20	69	109	39	35.78
10 h	R8	86	94	85	90.43
14 h	R6	57	78	7	8.97
14 h	R6 + 5	61	88	9	10.23
14 h	R6 + 10	68	105	34	32.38
14 h	R6 + 20	76	133	92	69.17
14 h	R8	87	245	217	88.57

Taken together, the fixed-day DAS snapshot analyses indicate that harvest timing and seed maturity are the dominant determinants of germination performance, while LED treatment differences are not consistently detectable at discrete time points—an outcome likely attributable to limited per-seed-lot test sizes (typically 5–6 seeds) and reduced statistical power when the dataset is partitioned into narrow fixed-day DAS subsets. The overall model using the full maturity gradient (Table S20) is therefore presented as the primary germination result, with fixed-day DAS analyses (Tables S21 and S23) serving to clarify maturity-driven trends and to contextualize the instability of discrete-day LED treatment contrasts under saturation or low-information conditions.

4. Discussion

In this study, the magnitude and consistency of the developmental responses observed in both cultivars indicate that photoperiod was the primary environmental factor regulating reproductive timing. As expected for a short-day crop, soybean grown under the 10 h photoperiod flowered and matured substantially earlier than plants exposed to longer photoperiods, demonstrating a strong inductive response to short-day conditions. This rapid flowering and maturation observed under 10 h of light are consistent with an inductive short-day signal that shortened the vegetative period and accelerated the transition to reproduction. Jähne et al. [34] demonstrated that soybean, classified as a short-day crop, flowered earlier under photoperiods of ≤ 12 h, with 10 h of light resulting in flowering approximately 23 to 24 days after sowing and maturity in approximately 77 days. The

study also employed staggered early harvests and found that germination improved as harvest was delayed from 56 to 77 days, thereby supporting the use of short photoperiods and early seed harvest in soybean speed breeding [34].

The 10 h exposure served as the treatment in the experiment that accelerated development the most; however, it resulted in low stem biomass and a moderate pod count when compared to those in field conditions. This pattern suggests that the rapid progression through phenological stages restricted the time available for canopy expansion, internode production, branching, and the proliferation of reproductive sinks before pod filling. Under the 10 h regime, the increased rate of generational turnover was associated with reduced biomass accumulation and pod production, thereby demonstrating a trade-off between developmental speed and reproductive output. This trade-off is highly relevant to breeding efforts, as the photoperiod that most effectively facilitates generation advancement may not coincide with that which best supports seed multiplication, plant biomass, or reproductive output. Alterations in photoperiod are essential during several developmental phases. Prolonged light periods enhance biomass growth and inhibit flowering by stabilizing repressor complexes such as the evening complex component J, via the E2-FKF1 complex, which relieves repression of the floral repressor *E1* and reduces the expression of floral promoters *GmFT2a* and *GmFT5a* [53]. Conversely, short-day conditions promote flowering by reducing *E1* expression and activating *GmFT2a* and *GmFT5a* [53,54]. The photoperiod sensitivity created by molecular feedback mechanisms involving regulatory elements such as E2 and the evening complex is crucial for crop acclimatization to varying latitudes [55]. A similar trend was reported in soybean by Chaudhary and Sandhu [17], in which exposure to red-blue light slightly hastened maturation. Elevated CO₂ levels primarily resulted in greater biomass production, more flowers, improved seed yield, and increased seed weight. This complex balance is further illustrated by Potts et al. [56], demonstrated that extended photoperiods could promote growth and flowering but may also reduce reproductive output. Wheat, durum wheat, barley, and *Brachypodium* exhibited significantly accelerated life cycles when subjected to a regime of 22 h of light followed by 2 h of darkness. However, wheat produced fewer seeds per spike under these conditions. Thus, the 10 h protocol is best interpreted as a generation-advance tool rather than a seed-bulking or biomass-production system.

Significantly, the 18 h delay in entering R1 resulted in increased plant height and enhanced stem dry weight, which was anticipated since prolonged vegetative growth is typically observed under noninductive daylengths. In soybean, extended or noninductive photoperiods may postpone the transition to flowering and prolong the vegetative developmental period. Long-day conditions activate the *E1*-related pathway, which represses flowering by decreasing the expression of *FT2a* and *FT5a* and thereby delays flowering [57]. Yang et al. [58] demonstrated that flowering is progressively delayed as daylength exceeds the critical photoperiod specific to each genotype. This extended pre-flowering phase promotes greater vegetative growth and increased accumulation of photosynthates before reproductive sinks are established. The increased plant height observed under the 18 h photoperiod may therefore reflect a prolonged vegetative phase, greater cumulative light exposure before the R1 stage, and continued stem elongation. Spectral composition may also influence plant architecture through red and far-red signaling. Phytochrome perception is regulated by red and far-red light, and PIF transcription factors play a crucial role in shade-avoidance responses and hypocotyl elongation [59]. A reduction in the red-light ratio is associated with enhanced elongation of internodes and petioles, whereas a higher proportion of blue light is associated with a more compact plant structure [60]. Variations in the absorption of red and blue wavelengths by photosynthetic pigments, together with their effects on photosynthetic efficiency, indicate that spectral light balance

can substantially affect plant physiological performance [61]. Nonetheless, because the LED treatments did not significantly alter R1 or R6 across photoperiods, the increased height and biomass observed under 18 h should be interpreted cautiously as arising primarily from the effect of photoperiod on the extension of vegetative growth. In this context, the LED spectra appear to function more as modifiers of morphology than as primary determinants of development.

By contrast, under 22 h, plants reached early reproductive stages (R1/R2) at approximately the same time (~28 DAS) nearly identical to that observed under 14 h (~27 DAS), but did not progress to R6. This pattern suggests that the critical night length threshold required to suppress flowering in these MG III–IV cultivars was not exceeded under the 22 h photoperiod—or that the accumulation of Pfr during the brief 2 h dark period was insufficient to completely inhibit floral induction. The subsequent failure to progress to R6 may reflect disruption of source–sink partitioning under near-continuous light, impaired phytochrome-mediated seed-fill signaling, or photo-oxidative stress during reproductive development. Continuous or near-continuous light may damage plants by disrupting circadian organization, carbohydrate balance, and photoprotective control. In general, higher light levels promote photosynthesis and plant growth; however, excessive light can lead to photoinhibition, oxidative stress, and impaired photosynthetic efficiency [62]. In addition, excessive light has been reported to induce photoinhibition, reactive oxygen species (ROS) formation, PSII damage, and an increased requirement for non-photochemical quenching (NPQ) and antioxidant protection mechanisms [63]. These effects may be particularly detrimental during pod and seed development, as reproductive sinks depend on a coordinated supply of assimilates from source leaves. Because the present experiment did not measure circadian markers, reactive oxygen species, non-structural carbohydrates, pod abortion, or assimilate transport, this interpretation remains mechanistic but tentative and should therefore be tested directly in future research. Consequently, future research should quantify these processes by chlorophyll fluorescence, reactive oxygen species markers, non-structural carbohydrate measures, pod abortion assessment, and the evaluation of photosynthesized material transportation.

Comparisons with other speed-breeding studies further highlight the sensitivity of soybean reproductive completion to photoperiod scheduling. These findings elucidate why soybean speed-breeding protocols differ, given that soybean is a short-day, photoperiod-sensitive crop, and that a constant long photoperiod can inhibit or delay flowering. Rajendran et al. [39] reported that prolonged photoperiods can prevent flowering in soybean and therefore employed a staged protocol comprising 16 h light and 8 h dark during early vegetative growth. Similarly, Aciksoz et al. [37] maintained a 12 h photoperiod until flowering, specifically the R1 stage, and only subsequently extended it to 22 h, thereby demonstrating that long-day conditions are more effective after flowering has been initiated. Under this post-flowering 22 h photoperiod, soybean plants reached physiological maturity approximately 50% faster than under the standard 12 h photoperiod. Accordingly, successful soybean speed-breeding protocols generally avoid applying a constant 22 h photoperiod throughout the entire life cycle and instead implement stage-specific photoperiod management to accelerate development. By contrast, the present 22 h treatment was maintained continuously from sowing onward, which may have permitted early floral initiation while preventing coordinated pod and seed development. Unlike the staged protocol developed by Aciksoz et al. [37], which introduced the 22 h photoperiod only after flowering (R1 stage), the present study maintained a constant 22 h photoperiod from sowing onward. This distinction is significant for protocol design, as long photoperiods may be beneficial after an inductive phase in some genotypes or systems, whereas a constant

near-continuous photoperiod appears to present risks for reproductive completion in the MG III–IV cultivars evaluated here.

Photoperiod-based acceleration in a short-day crop, such as soybean, remains challenging, particularly because soybean cultivars differ widely in phenological adaptation. Liu et al. [64] emphasized that soybean's broad geographic dissemination has resulted in substantial diversity in maturity timing and described the maturity group (MG) classification system, originally developed by the USDA Regional Soybean Laboratory [65] which has expanded to encompass early (MG 000) through late (MG X) groups [64]. Although 'Sonya' and 'Victoria' lack official maturity group (MG) classifications in Turkish registration documents, both cultivars were evaluated by the Turkish Seed Registration and Certification Center alongside MG III–IV standard cultivars during national registration trials. The MG III–IV standard cultivar 'Lider' (declared MG 3.8) reached 50% flowering at 35 and 29 days after sowing in Antalya and Adana, respectively, during 2018 trials, compared to 26 and 27 days for 'Sonya'. In 2021 registration trials in Türkiye, 'Lider' flowered at 39 and 23 days in Antalya and Adana, respectively, while 'Victoria' flowered at 37 and 21 days. Field observations from Antalya in 2023 further corroborated these findings, with 'Sonya' and 'Victoria' reaching flowering at 36.0 ± 1.96 and 35.3 ± 1.96 days after sowing (LSMean $\pm$ SE), respectively, consistent with reported MG III–IV phenotypes. These registration data and field observations provide phenotypic evidence supporting the approximate MG III–IV classification employed in this study. A secondary limitation should be the modest number of biological replicates per treatment ($n = 3$), which may have constrained statistical power to detect cultivar-specific differences in photoperiod sensitivity. Consequently, the absence of a statistically significant cultivar $\times$ photoperiod interaction should be interpreted cautiously, as null results do not definitively exclude subtle genotypic effects.

In a two-year study in China using 512 cultivars from multiple MGs, Liu et al. [64] quantified the flowering-to-maturity ratio (F/M; R1 to R8) and reported values for MG III–IV that align with the F/M ratios observed for 'Sonya' and 'Victoria' in our field trial (0.291 and 0.295, respectively). Similarly, Yang et al. [58], evaluating 72 genotypes spanning MG 0000–MG X under photoperiods from 12 to 20 h, showed that critical photoperiod decreases from MG 0000 to MG X and reported VE–R1 durations for MG III and MG IV under 14 h (24.6 and 28.7 d from emergence, respectively). Accounting for a typical germination and emergence period of 3–5 days under warm temperatures, these values correspond to approximately 27–34 DAS, a range that closely encompasses our 14 h estimates (~27 DAS). Under 18 h, Yang et al. [58] reported 71.2 and 81.6 d to flowering for MG III and MG IV, respectively, comparable to our observations under 18 h ('Sonya': 68.2 DAS; 'Victoria': 63.0 DAS). Taken together, these comparisons support that the responses observed in 'Sonya' and 'Victoria' are consistent with published MG III–IV behavior under intermediate-to-long photoperiods. It should be noted, however, that the maturity group assignments of 'Sonya' and 'Victoria' are based on phenotypic evidence from official registration trials rather than molecular characterization of the major maturity genes (E1–E4 and J). Although definitive genotypic confirmation was beyond the scope of the present study, the consistency between the official registration trials, our field observations, and published MG III–IV phenological responses provide confidence that these cultivars exhibit approximate MG III–IV behavior. Therefore, the photoperiod responses discussed here should be interpreted as representative of cultivars with approximate MG III–IV phenology rather than genetically confirmed MG III–IV genotypes. It should also be noted that the field experiment was intentionally established on 31 May because 'Sonya' and 'Victoria' were developed and officially registered for second-crop soybean production under Mediterranean conditions in Türkiye. Accordingly, the field trial was designed to reflect the recommended

production system for these cultivars. Furthermore, the phenological development observed under field conditions was consistent with the phenotypic characteristics reported during their official registration trials, supporting that the environmental conditions of the field experiment were representative of the target production environment.

Our results are also consistent with reports that short-day photoperiods reliably induce flowering in soybean under controlled environments. Jähne et al. [34] reported similar R1 timing under 12 h, 10 h, and 8 h photoperiods (~24 d) and concluded that lower red:blue ratios can reduce plant height without altering flowering time. In agreement, we found strong photoperiod effects on R1 and R6, limited LED treatment effects on developmental timing, and clear differences in plant height among LED treatments that varied in red:blue balance. Nagatoshi and Fujita [35] reported ~25 d to R1 under a 14 h photoperiod using fluorescent lighting at $\sim 220 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ with CO₂ supplementation, comparable to our observation of ~27 DAS at 14 h. Although CO₂ was not actively enriched in the present study, mean CO₂ concentrations in the growth chamber remained moderately elevated (approximately 500–600 ppm), likely attributable to chamber volume constraints and ventilation dynamics during the experimental runs.

In the present study, the effects of LED treatment were not detected for R1 or R6, whereas photoperiod exerted dominant control over developmental timing. Photoperiod functioned as the primary developmental switch, while LED spectral composition mainly influenced secondary growth and seed-quality traits. When photoperiodic signaling is strongly inductive or inhibitory, spectral effects may assume a secondary role. This interpretation is consistent with soybean speed-breeding studies demonstrating that short-day photoperiods strongly induce flowering, while the effects of LED spectra on plant architecture and productivity remain variable. Masangano et al. [38] employed an 8 h light/16 h dark regime because soybean is a photoperiod-sensitive short-day species, and red–white LEDs accelerated flowering and maturity relative to blue LEDs. However, Masangano et al. [38] also reported treatment-dependent differences in plant height, compactness, pod number, seed yield, and accession responses, thereby confirming that architecture and reproductive output depend on light spectrum, intensity, and genotype. Notably, a relatively high and uniform PPFD of 400 to 600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ was maintained across LED treatments. Under the 10 h photoperiod, R1 occurred at approximately 24.5 DAS, which falls within the range reported by Masangano et al. [38] under higher-intensity red–white lighting at 513 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. With respect to plant height, shorter plants were observed under LED-3 and LED-1, which had higher deep-blue fractions, whereas LED-4, with a lower deep-blue proportion, produced the greatest height, consistent with the established influence of red:blue balance on soybean architecture. Blue-light enrichment has been associated with changes in stomatal activity and plant growth characteristics. Trivellini et al. [60] reported that blue-light enhances the chlorophyll a/b ratio, increases photosynthetic activity, and regulates stomatal opening while reducing cell division and growth extension. The same study further indicated that a higher proportion of blue light is associated with a more compact growth habit and reduced plant height as blue-light levels increase. Trivellini et al. [60] additionally noted that a decrease in the red-to-far-red ratio promotes elongation of internodes and petioles through changes in phytochrome status. Liu and van Iersel [61] stated that red and blue wavelengths are absorbed more efficiently by photosynthetic pigments than green wavelengths and emphasized that photosynthetic responses depend on the interaction between the light spectrum and light intensity. Collectively, these findings suggest that spectral effects should be evaluated in conjunction with PPFD and overall light intensity. The comparison between field and chamber conditions should be interpreted as descriptive rather than causal because the two production systems differed in several environmental characteristics beyond photoperiod.

Although the controlled-environment chamber enabled precise regulation of photoperiod, temperature, and humidity, field-grown plants experienced unrestricted rooting volume, natural solar radiation, full-spectrum light with continuously changing spectral quality, natural air movement, fluctuating vapor-pressure deficit, and greater canopy space for branching and pod development. In contrast, chamber-grown plants were cultivated individually in 20 cm pots under controlled environmental conditions and therefore experienced root-volume limitation, restricted canopy expansion, and reduced whole-plant radiation interception. Consequently, the substantially greater stem dry weight and pod number observed under field conditions should be interpreted as reflecting the combined effects of these environmental differences rather than photoperiod alone.

Among these factors, root restriction is likely to have contributed substantially to the reduced vegetative growth and reproductive output observed under chamber conditions. Cassiano et al. [66] demonstrated that small pots restricted root and shoot growth and reduced leaf number, stem diameter, nodulation, and pod number, whereas larger pots improved leaf area and pod production. Poorter et al. [67] further supported this general pattern by showing that larger pot volume increases biomass production and that small pots can alter photosynthesis and experimental outcomes. Although no artificial *Bradyrhizobium* inoculation was performed in either environment, both field-grown and chamber-grown plants developed visible root nodules because the potting substrate contained non-sterilized soil collected directly from the experimental field. Therefore, differences in biological nitrogen fixation were unlikely to represent a major source of variation between the two production systems. Overall, the chamber-versus-field comparison should be regarded primarily as a practical benchmark illustrating the performance of speed breeding relative to conventional field cultivation, rather than as a direct evaluation of photoperiod effects alone. Future studies employing larger containers, standardized nutrient management, and multi-location, multi-year field validation will help disentangle the relative contributions of photoperiod, rooting volume, and other environmental factors to the observed differences between controlled-environment and field-grown soybean plants. Therefore, pot or tray size should be considered when interpreting soybean speed-breeding effects on architecture and yield-related traits. In addition, field observations were based on only four sampled plants per cultivar and originated from a single growing season at a single field location, resulting in greater uncertainty and correspondingly larger standard errors for several field-derived estimates. Consequently, quantitative comparisons between field and chamber conditions should be interpreted as descriptive rather than definitive because the lower field replication and limited field sampling reduced the precision and generalizability of the estimated field means. Future studies employing larger and more balanced field sample sizes across multiple seasons and locations would provide more robust estimates of environmental differences.

Environmental conditions and LED treatment showed a greater impact on the overall lipid content than on the relative fatty acid composition. This distinction is biologically plausible because total soybean seed oil concentration reflects broader carbon allocation during seed development. Soybean seed composition averages 18 to 22% oil and 36 to 42% protein [68], and a well-documented inverse correlation exists between seed oil and protein content, reflecting metabolic competition for shared carbon precursors during seed development [69]. Oil accumulation is also closely coordinated with carbon metabolism and nutrient partitioning, and environmental conditions during reproductive growth may generate differences in seed quality [69,70]. In addition, variation in oil concentration among environments depended mainly on maturity group effects, indicating that both genetic background and environmental conditions contribute to total oil concentration [70]. In contrast, the relative proportions of individual fatty acids are more directly governed by

fatty acid biosynthetic and modification pathways. α -Linolenic acid (ALA) is synthesized through the insertion of a $\text{cis}\Delta 15/\omega 3$ double bond into linoleic acid, and these reactions are catalyzed by the fatty acid desaturases FAD3, FAD7, and FAD8 [71]. FAD3 and FAD7/FAD8 encode integral membrane proteins localized to the endoplasmic reticulum or chloroplast membranes, and FAD3 expression is highly regulated during development [71]. Accordingly, total oil concentration is influenced by carbon metabolism, nutrient partitioning, maturity group, and environmental conditions, whereas fatty acid composition is more directly regulated by specific desaturase enzymes and fatty acid biosynthetic pathways [71]. In the present study, 'Sonya' consistently exhibited a higher oil concentration than 'Victoria', supporting a strong genotypic component, while the absence of a photoperiod $\times$ cultivar interaction suggests that cultivar differences in oil accumulation were relatively stable across the evaluated environments. The overlapping CLR-PCA ellipses among LED treatments further support the interpretation that LED spectra affected oil quantity more clearly than proportional fatty acid composition. Oil concentration and fatty acid composition analyses were constrained by the labor-intensive nature of laboratory-based chemical measurements, resulting in a modest number of biological replicates. While statistically significant treatment effects were detected, future studies with expanded sample sizes would enhance precision in estimating treatment effects on soybean seed oil quality.

Harvest time and seed maturation were the primary variables influencing germination; nevertheless, the overall maturity-gradient model indicated a notable influence of the LED treatment, with LED-3 resulting in the greatest adjusted emergence rates for the seeds. Although LED spectra did not substantially alter developmental timing, maternal light quality may have influenced seed physiological maturity and vigor. Maternal environmental conditions during seed development can affect seed vigor, dormancy, germination, and longevity. Reed et al. [72] explain that seed aging depends on environmental storage conditions, seed genetics, and the maternal environment, and further indicate that genotype and environment during seed development influence ABA biosynthesis and dormancy depth. Nguyen et al. [73] additionally demonstrate that environmental conditions during seed maturation strongly affect seed quality and that seed longevity is associated with the genetic regulation of dormancy-related loci. Therefore, changes in the maternal growth environment may affect reserve accumulation, hormonal balance, desiccation tolerance, and subsequent germination performance. LED-3 may thus have provided a maternal environment that improved reserve deposition or desiccation tolerance in the tested seed lots, particularly when immature seeds were harvested from R6 onward. However, because the fixed-day analyses showed inconsistent LED effects at discrete harvest times and the speed-breeding protocol inherently produced relatively small biological seed lots, the apparent germination advantage associated with LED-3 should be regarded as promising but preliminary. Accordingly, this observation should be interpreted with caution and verified in future studies using larger biological seed lots specifically designed for germination testing.

An important consideration of this study is that photoperiod treatments were conducted as sequential runs within a single growth chamber rather than concurrently. As a result, photoperiod effects may be partially associated with temporal variation between runs. However, environmental conditions, irrigation, substrate, nutrient management, target PPFD, and sanitation procedures were carefully standardized to minimize variability. While these measures support the consistency of the experimental conditions, future studies employing concurrent photoperiod treatments in independent growth chambers or fully replicated randomized designs would further strengthen causal interpretation. A second consideration is that seed weight was not measured. Metrics such as 100-seed weight or individual seed weight could provide additional insight into seed filling and

potential treatment-related differences in seed quality. Due to limited seed availability, particularly for immature harvests, available seeds were prioritized for germination and oil-content analyses. Future work incorporating seed weight measurements alongside physiological and biochemical assessments would provide a more comprehensive evaluation of seed quality.

Overall, the present results are consistent with a two-tier interpretation of light control in soybean speed breeding. Photoperiod determined the developmental trajectory: 10 h and 14 h supported rapid reproductive completion, 18 h delayed development and promoted vegetative growth, and 22 h permitted early reproductive initiation but failed to support seed fill. LED spectra then acted mainly on secondary traits such as plant architecture, stem biomass, oil concentration, and emergence potential. For breeding programs, this means that protocol choice should be aligned with the immediate objective. A 10 h photoperiod is appropriate when the priority is rapid generation advance, whereas seed multiplication, physiological seed quality, or trait phenotyping may require a less accelerated protocol, larger rooting volume, staged photoperiod scheduling, or subsequent field/greenhouse seed increase [18,34,37–39,74]. Future studies should evaluate these interpretations using repetitive or temporally replicated blocks, bigger pot dimensions, and increased rooting volumes, including hydroponic systems where suitable. These investigations should include direct assessments of photosynthesis, E-gene genotyping, leaf carbohydrate levels, oxidative stress indicators, dry seed mass, and transcriptomic analysis of genes associated with flowering and lipid pathway regulation.

5. Conclusions

Photoperiod constituted the principal determinant of developmental timing in soybean under the controlled-environment speed-breeding conditions examined and exerted the strongest influence on the transition to key reproductive stages. The 10 h photoperiod resulted in the most rapid progression to R1 and R6 and was therefore suitable for rapid generation turnover and efficient cycle advancement, whereas the constant 22 h photoperiod permitted early floral initiation but did not support the completion of reproduction or the attainment of full reproductive maturity. This distinction confirms that floral initiation alone is insufficient to establish an effective soybean speed-breeding protocol, because successful protocol design must also ensure continued reproductive development through seed set and maturation. LED spectral composition functioned primarily as a secondary factor that modulated plant architecture, biomass accumulation, seed oil concentration, and germination performance rather than as a primary determinant of flowering initiation or maturity timing under these controlled conditions. Maximum developmental acceleration occurred at the expense of biomass accumulation and pod production, indicating that rapid generation cycling entails a clear trade-off with reproductive productivity, including reduced plant size and lower pod yield. For breeding programs, the 10 h protocol appears to be the most suitable for rapid generation advancement and efficient turnover, whereas seed multiplication and productivity assessment may require complementary greenhouse- or field-based multiplication steps in order to ensure an adequate seed supply and a more representative evaluation of agronomic performance.

These findings provide a practical and directly applicable framework for soybean breeding programs seeking to balance rapid generation turnover, seed quality, and overall plant productivity in controlled environments, particularly in the selection of protocols for both generation advancement and seed production. Future optimization should incorporate cultivar-specific photoperiod sensitivity, carefully staged light schedules across developmental phases, adequate rooting volume to support healthy growth, and spectral

regimes that promote seed vigor, germination performance, and seedling establishment while maintaining the rapid completion of reproductive development.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/agronomy16151404/s1>, Tables S1–S23: Statistical outputs supporting the main text, including ANOVA and Tukey HSD results, photoperiod-specific least squares means (LSMeans $\pm$ SE) and compact letter display (CLD) groupings for days to R1 by LED treatment, estimated marginal means (EMMs) and CLD groupings for maximum plant height and pod number by LED treatment, and Type III Wald χ^2 test results for pod number across environments.

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