Original scientific paper
Journal of Central European Agriculture, 2026, 27(2), p.476-490
DOI: /10.5513/JCEA01/27.2.4949

Soybean maturity genes effect on growth parameters and non-structural carbohydrate accumulation under different photoperiods

Dmytro HLUSHACH (✉), Yuliia YUKHNO, Olha AVKSENTIEVA

V. N. Karazin Kharkiv National University, 4 Svobody Sq. 61022 Kharkiv, Ukraine

✉ Corresponding author: hlushach2019pg@student.karazin.ua

Received: July 22, 2025; accepted: January 14, 2026

ABSTRACT

The study evaluates the role of photoperiod sensitivity genes (*E-genes*) in forming growth traits and the accumulation of soluble carbohydrates in soybean (*Glycine max* (L.) Merr.) leaves under different day lengths. Four genotypes, including the cv. Clark and three nearly isogenic lines (NILs) differing in the alleles at the *E1*, *E2*, and *E3* loci were cultivated under long-day (16 hours) and short-day (9 hours) conditions. Growth parameters such as relative growth rate (RGR) and net assimilation rate (NAR), along with the content of soluble carbohydrates in the leaves (monosaccharides and oligosaccharides), were determined at developmental stages V3 to V5. Short-day plants (Clark and L80-5879) demonstrated higher RGR and NAR values under long-day conditions, which was caused by increased photosynthetic activity, especially in cv. Clark (has recessive *e1* allele alongside dominant *E2* and *E3* alleles). In contrast, short-day conditions decreased RGR and NAR, redirecting resources towards reproductive development. Neutral-day plants (L63-3117 and L71-920) demonstrated higher stability in growth and carbohydrate content across both photoperiods. Monosaccharide content increased in neutral-day lines under both photoperiods during the V3–V5 developmental period, while oligosaccharide levels decreased, indicating more stable carbohydrate mobilization compared to short-day lines. These results highlight different adaptive strategies: short-day lines show enhanced vegetative growth under long photoperiods, whereas neutral-day lines maintain metabolic stability regardless of day length. Understanding these features will help to optimise soybean cultivation more effectively in different climatic conditions.

Keywords: *Glycine max* (L.) Merr., near isogenic lines, *E-genes*, photoperiodic sensitivity, soluble carbohydrate, growth analysis

INTRODUCTION

According to the Food and Agriculture Organization of the United Nations, soybean (*Glycine max* (L.) Merr.) is an economically important crop that ranks among the leading in global production volumes, particularly among oilseed crops (FAO, 2024). Soybean is a source of valuable plant protein, oil, vitamins, essential amino acids, and other beneficial substances, and is used for human and animal nutrition, biodiesel production, and soil nitrogen enrichment (Ali et al., 2020). Soybean is evolutionarily a short-day plant and is sensitive to photoperiodic influence (Wang et al., 2022). It is known that the photoperiod determines the rate of plant development and regulates the transition from the vegetative to the generative stage (Cober et al., 2014). The photoperiod enables plants to synchronize growth and developmental processes with environmental rhythms (circadian and seasonal) and to more effectively adapt to biotic and abiotic stresses (Gupta et al., 2022; Staniak et al., 2023). The photoperiodic signal not only controls the transition to flowering and maturation but also affects other physiological, biochemical, and ontogenetic processes (Osnato et al., 2022). In soybean, as a photoperiod-sensitive model organism, the role of photoperiod has been shown in the regulation of numerous processes: initiation of flowering (Cober et al., 2014; Lu et al., 2014), stem growth characteristics (Cao et al., 2017; Hussain et al., 2019), rate of node formation (Ort et al., 2022), leaf morphology (Li et al., 2021), photosynthetic efficiency, biosynthesis of non-structural carbohydrates, sucrose (Kumudini, 2002; Dogra et al., 2015), pod setting (Taniguchi et al., 2020; Sun et al., 2024), yield, biochemical composition of seeds (Zhmurko and Al-Hamadeni, 2019), and adaptability (Staniak et al., 2023).

To date, ten maturity genes, *E1–E10*, and *J* have been identified in *Glycine max* (L.) Merr., which determines photoperiodic sensitivity, the rate of transition to flowering, and the maturation of pods after flowering. Among the quantitative trait loci (QTLs) responsible for flowering time and earliness, the gene loci *E1–E4* and *E9* are especially important and have been identified through precise genetic mapping (Cao et al., 2017; Li et al., 2021). *E1* has the strongest effect on soybean flowering – it encodes a transcription factor that acts as a repressor of flowering under long-day conditions. The soybean genome contains two *E1* homologs, *E1La* and *E1Lb*, which are located 10 640 base pairs apart on chromosome 4 (Chr. 4). The *E1* and *E1L* genes suppress flowering by repressing the *GmFT2a* gene, an ortholog of *FLOWERING LOCUS T (FT)* identified in *Arabidopsis thaliana*, which is a flowering inducer (Li et al., 2021). *E2* has been identified as an ortholog (*GmGIa*) of the *Arabidopsis GIGANTEA (GI)* gene. Two alleles of *E2* are known – a dominant, functional *E2* allele that delays flowering by repressing *GmFT2a*, and a recessive *e2* allele that promotes early flowering by lifting this repression (Li et al., 2021). *E3* and *E4* were identified and functionally confirmed as phytochrome A (PhyA) genes – *GmPhyA3* and *GmPhyA2*, respectively (Zhang et al., 2021). Both were identified via genetic analysis of flowering responses to artificially induced long-day conditions. *E3* is involved in the control of flowering under long-day conditions with a high red to far-red (R : FR) quantum ratio, whereas *E4* is responsible for flowering responses under long-day conditions with a low R : FR ratio. *E3* functions across a wide range of latitudes, whereas allelic differences in *E4* are observed only at high latitudes. Other maturity loci (*E5–E8*, *E10*, *J*) have been mapped but are less characterized; their molecular identities and specific roles continue to be investigated (Dissanayaka et al., 2016; Luo et al., 2021). In contrast, the *E9* gene was identified in populations derived from crosses between wild and cultivated soybean as *GmFT2a*, which is a flowering inducer. The *e9* allele is rare and phenotypically delays flowering while maintaining vegetative growth in soybean plants (Kong et al., 2014).

Currently, active research is being conducted to investigate the nature of photoperiodic sensitivity. Various authors explore the interactions of *E-series* genes with environmental factors in the regulation of growth parameters and carbohydrate metabolism (Miranda et al., 2020; Hlushach and Avksentieva, 2024; Raievska and Schogolev, 2024). Carbohydrates are produced in the plant organism during photosynthesis – the primary assimilation process that determines the realization of the plant's productivity potential (Sachin et al., 2024). Assimilates, mainly represented by soluble carbohydrates in the plant, can serve as the primary energy and structural material for biomass accumulation during the vegetative phase or as an energy source for the processes of flowering, fertilization, and fruit maturation during the generative stage of development (Kumudini, 2002). However, some carbohydrates also exhibit signalling functions. In addition to photoperiodic influence, sucrose and other soluble carbohydrates play important roles as signalling molecules in the regulation of flowering induction. It is known that the photoperiodic signal is perceived by the leaf in the plant body and is transduced as a long-distance signal in the form of FT protein transcript, which is currently considered the florigen, to the shoot apical meristems, where it initiates floral morphogenesis programs. Under inductive conditions, florigen acts synergistically with soluble carbohydrates: for example, in *Arabidopsis*, it has been shown that sucrose in the leaf phloem stimulates florigen formation, while in the apical meristem of the stem, this role is played by another carbohydrate-trehalose-6-phosphate (Cho et al., 2018). Other studies show that under long-day conditions, the daily amplitude of sucrose levels affects the expression of the *MIPS1* gene, which promotes vegetative plant growth and, thus, delays the transition to the generative development phase (Wang et al., 2023).

Thus, the photoperiod, as a regulatory factor in plant development stages, facilitates the selection of an adaptive strategy by the plant organism to specific photoperiodic conditions and the influence of other environmental factors through interaction with the plant genotype (Hussain et al., 2020). This is also manifested in the regulation of assimilation processes that determine the plant's metabolic status. Understanding how *E-series* genes affect carbohydrate content and the growth of plants of different photoperiodic groups under varying day lengths is of fundamental importance and essential for optimizing soybean productivity across different climatic regions. Therefore, this study aimed to determine the role of *E* gene alleles, which determine photoperiodic sensitivity in soybean, in the regulation of growth parameters, synthesis of soluble carbohydrates, and the selection of adaptive strategies of photosynthetic processes under different photoperiodic conditions.

MATERIALS AND METHODS

Plant materials

Four genotypes were used in this study – the cultivar Clark and near-isogenic lines (NILs) of soybean (*Glycine max* (L.) Merr.) developed within the genetic background of this cultivar. The isolines differ in the *E* alleles, which determine the photoperiodic response and the maturity period after flowering. Near-isogenic lines represent an informative model system for the analysis of the functional effects of different alleles within a homogeneous genetic background. The allelic composition of the *E* loci in the near-isogenic lines was established in earlier classical genetic studies during the development of the isoline collections and is reported by Tasma and Shoemaker (2003) and presented in Table 1. The manifestation of this photoperiodic response was confirmed through phenological observations under field cultivation conditions at the experimental research site of the Department of Plant and Microorganism Physiology and Biochemistry of V. N. Karazin Kharkiv National University, Kharkiv (geographical latitude – 50° N). These lines were originally developed by the Agricultural Experiment Station of the University of Illinois in collaboration with the National Institute of Food and Agriculture of the United States Department of Agriculture (www.nifa.usda.gov). The NIL seeds used in the research were provided by the National Center for Plant Genetic Resources of Ukraine, Kharkiv (https://yuriev.com.ua), which maintains the purity of the lines.

Table 1. Isogenic lines (NILs) for genes controlling photoperiod sensitivity in soybeans, created in the genotype of the Clark variety

Isolines	Alleles at the *E* loci	Photoperiodic reaction
Clark	*e1E2E3E4e5E7*	short-day plant (SDP)
L 80-5879	*E1e2e3E4e5E7*	short-day plant (SDP)
L 63-3117	*e1e2E3E4e5E7*	day-neutral plant (NDP)
L 71-920	*e1e2e3E4e5E7*	day-neutral plant (NDP)

Experiment design

Field experiments were conducted at the experimental site of the Department of Plant and Microorganism Physiology and Biochemistry of V. N. Karazin Kharkiv National University during the 2023 – 2024 growing seasons (Eastern Forest-Steppe of Ukraine, 50° N latitude). The soil type was a leached heavy loamy chernozem. No fertilizers or bacterial preparations were applied to the plants. Sowing was performed manually on plots of 1 m^2, with three biological replicates for each line, at the end of May. Each isoline plot consisted of six parallel rows, each 1 meter in length, with 20 seeds manually sown per row. After emergence and up to the third true leaf stage (V3), the plants were grown under natural long-day conditions (in Kharkiv, 50° N – 16 hours of daylight). Upon reaching the V3 stage, experimental plants of each isoline were subjected to photoperiodic induction under short-day conditions for 14 days. The short-day photoperiod was artificially created by placing the plants in lightproof chambers from 5:00 p.m. to 9:00 a.m. (photoperiod duration: 9 hours). Control plants continued to be grown under natural long-day conditions (photoperiod duration: approx. 16 hours).

Growth analysis

At the third (V3) and fifth (V5) true leaf stages, measurements were taken of the dry mass of aboveground plant organs, the number of leaves per plant, and total leaf area. Leaf area was calculated by using leaf image analysis (image processing). Based on these parameters, assimilation indices were calculated according to Hunt (2017):

$$\mathrm{RGR} = \frac{\ln \mathrm{W}_2 - \ln \mathrm{W}_1}{\mathrm{t}_2 - \mathrm{t}_1}$$

where RGR – relative growth rate (mg/g per day), W_2 and W_1 represent plant dry mass (mg) at time t_2 and t_1 (day).

$$\mathrm{NAR} = \frac{W_2 - W_1}{\mathrm{t}_2 - \mathrm{t}_1} \times \frac{\ln \mathrm{L}_{\mathrm{a}2} - \ln \mathrm{L}_{\mathrm{a}1}}{\mathrm{L}_{\mathrm{a}2} - \mathrm{L}_{\mathrm{a}1}}$$

where NAR – net assimilation rate (mg/cm^2 per day), W_2 and W_1 represent plant dry mass (mg) at time t_2 and t_1 (day); and La_1 and La_2 represent the total leaf area (m^2) per plant at time t_1 and t_2.

Determination of carbohydrate content in leaves

The content of reducing carbohydrates in fixed plant material was determined using a micromethod based on the reaction with potassium ferricyanide $K_3[Fe(CN)_6]$ (Porro et al., 1981). Carbohydrates were extracted twice from dry, fixed samples (pooled sample) using 80% ethanol in a water bath at 70 °C for 30 minutes. After cooling, the extract was centrifuged for 10 minutes at 3000 rpm. The total extract volume was 25 ml. For the reaction, 0.2 ml of extract and 1.8 ml of distilled water were added to 1 ml of potassium ferricyanide reagent (g/l: $K_3[Fe(CN)_6]$ – 1.65; Na_2CO_3 – 10). The mixture was incubated in a boiling water bath at 100 °C for 15 minutes. After cooling, 2 ml of ferric sulfate solution (g/l: $Fe_2(SO_4)_3$ – 1, concentrated H_2SO_4 – 10 ml) was added. The monosaccharide content was assessed by the intensity of blue coloration using a Halo DB-20 spectrophotometer (Dynamica Scientific Ltd, UK) at 690 nm. The concentration of reducing sugars was determined using a calibration curve prepared with different concentrations of glucose (Sigma).

To quantify the content of oligosaccharides, the total content of water-soluble non-structural carbohydrates was measured. For this, the extract was pre-treated with 1 M HCl for hydrolysis. The resulting solution was neutralized with 1 M NaOH, and the total sugar content was determined by the same method. The content of oligosaccharides was calculated as the difference between the total sugar content and the monosaccharide content.

Statistical data analysis

Statistical analysis of the obtained data was made using the Statistica 10 software package (StatSoft Inc., 2011, USA). One-way analysis of variance (ANOVA) was used to assess the significance of differences between group means. For multiple group comparisons, one-way ANOVA followed by Tukey's post hoc test was applied to identify statistically significant differences between individual groups ($P<0.05$). Data are presented as means ± standard deviations (x ± SD) in figures and tables.

To classify isogenic lines according to their photoperiodic response, K-means cluster analysis was performed based on Euclidean distance using 12 parameters (growth and metabolic indicators) measured at the V5 stage relative to V3. The clustering results were visualized using hierarchical heatmaps.

To assess relationships between the alleles at the *E1*, *E2* and *E3* loci and growth parameters (RGR, NAR) as well as carbohydrate metabolism (monosaccharide and oligosaccharide content) under long-day conditions, Spearman's rank correlation analysis (ρ) was used. Spearman's coefficient was selected due to the categorical nature of the alleles (dominant/recessive) and the potential non-linearity of associations with the quantitative traits of growth and carbohydrate metabolism. Correlations were considered statistically significant at $P<0.05$.

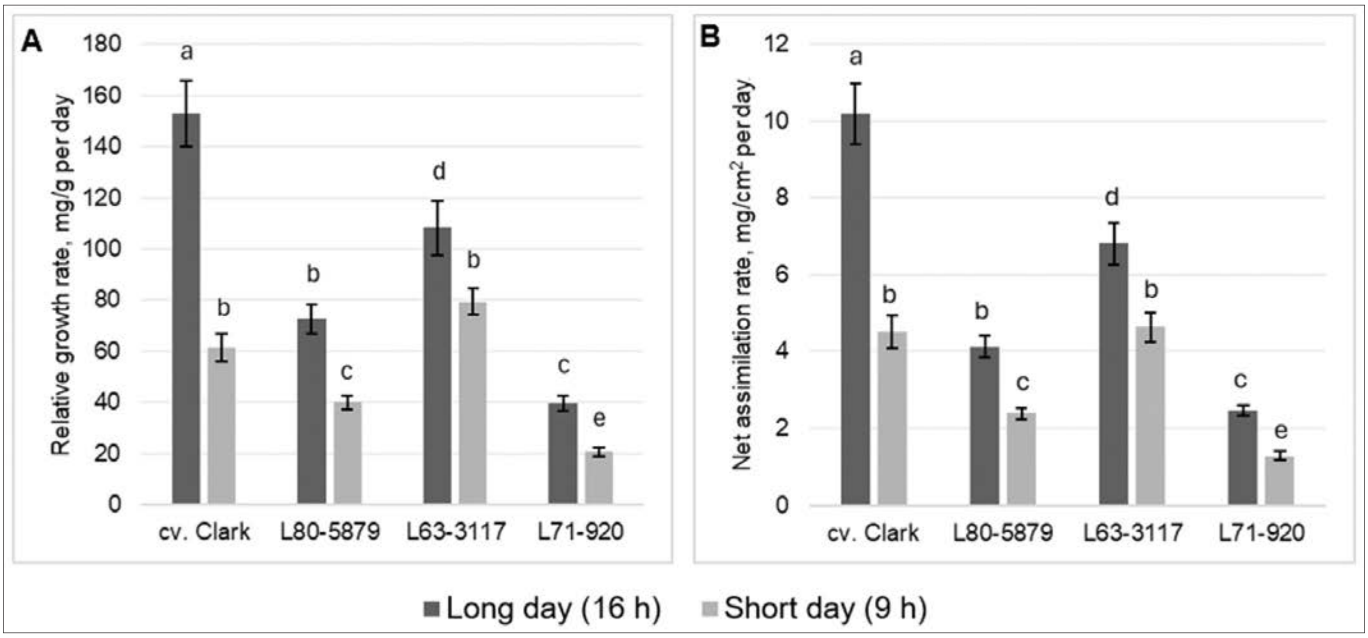
RESULTS AND DISCUSSION

Growth characteristics of soybean isolines under different photoperiod conditions

Plant size – and thus growth processes – is a critical factor for plant survival and reproduction in nature. The relative growth rate (RGR), defined as the rate of new dry mass accumulation per unit of existing dry mass, is a key determinant of plant competitiveness (Shipley, 2006). RGR serves as an indirect measure of resource acquisition rate, and numerous studies have shown that an increased RGR during the vegetative phase enhances crop productivity (Sachin et al., 2024). The faster a plant accumulates biomass, the more carbon becomes available for root and shoot development, enabling improved access to light and soil nutrients, thereby further enhancing biomass accumulation.

Analysis of the relative growth rate (RGR) revealed a significant decrease in RGR in soybean isolines differing in allelic states at the *E* loci under short-day (SD) conditions compared to long-day (LD) conditions throughout the experiment (from stage V3 to V5; Figure 1). At this stage, the day length reduction leads to a smaller leaf area (Yukhno et al., 2024), which may contribute to the observed decrease in RGR. However, RGR levels were influenced not only by photoperiodic conditions but also by the combination of *E* alleles present in the studied soybean isolines, which determines their photoperiod sensitivity. For instance, the cultivar ‘Clark’ (*e1E2E3E4e5E7*) exhibited the highest RGR under LD and the greatest reduction under SD (approximately 60%), suggesting a strong dependence of growth processes on day length. This may be associated with the presence of the recessive *e1* allele in combination with dominant *E2*, *E3*, and *E4* alleles, which may promote an increase in total leaf area and the involvement of younger leaves in photosynthesis, resulting in more effective biomass accumulation under LD conditions.

In the L80-5879 isoline (*E1e2e3E4e5E7*), RGR was significantly lower under both LD and SD compared to the Clark cultivar, although both exhibit short-day responses. Upon photoperiod reduction to 9 h, this isoline also demonstrated a ~45% decrease in RGR relative to its LD value (Figure 1A).



Note: comparisons were made between different isolines and photoperiodic conditions. Different letters indicate statistically significant differences based on Tukey’s post hoc test ($P < 0.05$).

Figure 1. Growth parameters of soybean isolines differing in the alleles at the E loci during the experiment (from developmental stage V3 to V5) under different photoperiod conditions (Long day – 16 h, Short day – 9 h; n = 10, x ± SD): A – relative growth rate (RGR); B – net assimilation rate (NAR)

The L63-3117 isoline (*e1e2E3E4e5E7*) showed the highest RGR under SD conditions. This may indicate a neutral photoperiodic response and suggest a higher adaptability of its physiological and biochemical processes to shorter photoperiods. This is further supported by the smallest observed difference between LD and SD RGR values (~26%).

The L71-920 isoline (*e1e2e3E4e5E7*) had the lowest RGR among the studied isolines under LD and showed a significant decrease under SD (approximately 48%). Despite its neutral photoperiodic response, this isoline showed a high sensitivity to day length reduction, likely requiring more light resources to maintain optimal growth. Such differences in growth response to different photoperiod lengths may be due to the presence in the genotype of this isoline of the recessive allele *e1* against the background of recessive alleles *e2* and *e3*. On the other hand, the recessive alleles cause the shortest duration of the vegetative phase among all lines under the influence of both long and short photoperiods (Table 2), which may affect the reduction of the rate of accumulation of newly formed dry matter to the already existing one. This, in turn, may be the reason for the very low RGR values, both on long and short days.

Since RGR changes in relation to the activity of two processes – photosynthesis and respiration (Lamont et al., 2023), at the end of the vegetative phase and during the transition to the generative phase (in soybean isolines – at developmental stage V5–V6 under short-day conditions), a decrease in RGR is mainly observed. This may be caused by an increase in respiration intensity relative to assimilation processes. On the other hand, it may also be related to the fact that the biomass accumulated by plants is mainly represented by structural rather than metabolically active tissues (Blumstein et al., 2024). Therefore, all these changes do not contribute to plant growth under short-day conditions and lead to a decrease in RGR during the experiment, which likely allows soybean isolines to regulate the direction of assimilate distribution between vegetative growth and the initiation and development of generative organs.

It is considered that the relative growth rate (RGR) depends on two indicators that are mathematically its components – leaf area ratio (LAR) and net assimilation rate (NAR). Thus, RGR is a function of the size (or LAR) and efficiency (or NAR) of the plant's photosynthetic apparatus (Hunt, 2017). The leaf area ratio (LAR) is an indicator of how efficiently the plant utilizes its photosynthetic resources. It was previously shown (Yukhno et al., 2024) that in all studied lines, when grown from developmental stage V3 to V5 under natural photoperiodic conditions (LD – 16 hours), the LAR level was quite high and nearly the same, except for the cv. Clark, which had the lowest LAR value (Yukhno et al., 2024). Under the influence of a short photoperiod (SD – 9 hours), a significant decrease in LAR was observed in the cv. Clark and isoline L80-5879, while in the NDP isolines, on the contrary, either an increase in LAR was noted (in isoline L63-3117) or no significant changes were detected (in isoline L71-920), relative to values observed under long-day conditions. This may indicate the presence of different adaptation strategies of the photosynthetic apparatus in soybean near-isogenic lines to different photoperiod durations, which is partly determined by the combination of *E* alleles in their genotypes.

Table 2. Vegetative phase duration of soybean NILs under long- and short-day conditions (days)

Isolines	Long day (16 hours)	Short day (9 hours)	Photoperiodic reaction
cv.Clark	68.0 ± 1.8	57.8 ± 3.1*	SDP
L80-5879	58.5 ± 2.9	47.5 ± 2.1*	SDP
L63-3117	52.8 ± 2.5	48.5 ± 3.4	NDP
L71-920	37.5 ± 1.9	36.3 ± 2.9	NDP

Note: SDP – short-day plants; NDP – neutral-day plant.

Comparisons were made within each isogenic soybean line between the variant “Short-day” and “Long-day”. Significant differences between the average values in the “Short day” and “Long day” columns for each isogenic line are marked with symbols “*” based on one-way ANOVA ($P<0.05$). Based on the results, the type of photoperiodic response of each isoline is indicated in the 'Photoperiodic reaction' column.

The net assimilation rate (NAR) is the physiological component of RGR, as it shows the daily net photosynthesis rate of the plant and characterizes the efficiency of the assimilation apparatus. Essentially, this indicator is a complex physiological variable associated with both photosynthesis and respiration rates and allows comparison of the efficiency of dry mass accumulation per unit of photosynthetic surface in plants (Li et al., 2016). According to the data obtained, differences in NAR levels (Figure 1, B) in the studied soybean isolines under different photoperiod durations showed similar patterns to RGR (Figure 1, A). That is, under long-day conditions, all lines showed significantly higher NAR values than under short-day conditions. The significant difference in NAR values between photoperiod durations was observed in the cv. Clark (a decrease of approximately 56% under the short-day). The smallest difference in NAR values between long- and short-day conditions was observed in the photoperiod-neutral isoline L71-920, which has the recessive alleles *e1*, *e2* and *e3* (Figure 1, B). At the same time, this isoline showed the lowest NAR level among all studied soybean isolines. The presence of the recessive alleles (*e1*, *e2* and *e3*) results in the production of nonfunctional proteins, which leads to the removal of repression from the *GmFT2a* under non-inductive photoperiodic conditions (long day). *GmFT2a* acts as a signal integrator and ensures the initiation of the flowering transition (Zhang et al., 2021).

The carbohydrate content in soybean leaves

Soluble carbohydrates are the main photosynthates of plants, which, on the one hand, are a source of carbon for biomass accumulation and construction of plant organs, and on the other hand, are a substrate for energy metabolism. Therefore, they can indicate a certain energy status of the plant (Kumudini, 2002). This especially applies to the group of oligosaccharides, including the main transport carbohydrate of plants – sucrose. Soluble carbohydrates, mainly monosaccharides and their derivatives, can be involved in various metabolic pathways and participate in the transduction of various signals (Cho et al., 2018).

On the other hand, the level of soluble non-structural carbohydrates primarily depends on the efficiency of the photosynthetic apparatus of the leaves and the enzymes responsible for the synthesis of oligosaccharides from monosaccharides. In addition, their content also depends on environmental conditions and the load of certain stress factors. At the same time, the content of photosynthates depends on a number of metabolic processes that are regulated by daily rhythms through the work of the circadian clock. Therefore, both the photoperiodic signal and the alleles at the *E* loci may be involved, along with other processes, in the regulation of the accumulation, export, and redistribution of assimilates in the plant organism.

All studied isolines were grown under identical photoperiodic conditions up to the V3 developmental stage. However, according to the obtained results, they slightly differed in the content of soluble non-structural carbohydrates in the leaves depending on the *E* alleles present in their genotype. Thus, the content of monosaccharides in the leaves at the V3 stage was the highest in the short-day cv. Clark (53 mg/g) and the lowest in the day-neutral isoline L63-3117 – 42.5 mg/g dry weight (Table 3). Throughout the experiment, in all studied soybean isolines, the content of monosaccharides in the leaves changed depending on the photoperiod length and the genotype of the isoline (Table 3). Under long-day (16-hour) conditions, an increase in monosaccharide content was observed in all isolines except for the cv. Clark, which has the recessive *e1* allele. The largest increase was observed in the isoline with the dominant *E3* allele in the genotype (L63-3117), by approximately 30% compared to the V3 stage. In cv. Clark plants, the monosaccharide content under long-day conditions did not change significantly throughout the experiment. Under short-day conditions at the V5 stage, an opposite reaction of different photoperiodic groups was observed. The short-day cv. Clark and the isoline L80-5879 showed a significant decrease in monosaccharide content, while the day-neutral lines L63-3117 and L71-920 demonstrated an increase in monosaccharide levels.

Table 3. Dynamics of the content of soluble carbohydrates in NILs soybean leaves under the influence of different photoperiods during the V3-V5 development period (n = 10, x ± SD)

Isolines	Parameter	Development stage – V3	Development stage – V5			
			Long day (16 h)	Δ V5 (LD) vs. V3, %	Short day (9 h)	Δ V5 (SD) vs. V3, %
cv. Clark	Monosaccharides	53.0 ± 1.0^{a}	54.1 ± 0.5^{a}	2.1	48.3 ± 1.3^{b}	-8.9
	Oligosaccharides	23.3 ± 4.0^{a}	17.4 ± 1.0^{b}	-25.3	21.3 ± 1.1^{a}	-8.6
	Total	76.4 ± 5.5	71.5 ± 6.5	-6.4	69.6 ± 4.7	-8.9
L80-5879	Monosaccharides	48.4 ± 0.4^{a}	52.7 ± 0.3b	8.9	43.3 ± 0.6c	-10.5
	Oligosaccharides	18.2 ± 0.3	15.9 ± 1.9	-12.6	17.1 ± 1.0	-6.0
	Total	66.6 ± 5.7	68.6 ± 5.6	3.0	60.4 ± 4.5	-9.3
L63-3117	Monosaccharides	42.5 ± 1.5^{a}	55.5 ± 0.6b	30.6	51.5 ± 1.2c	21.2
	Oligosaccharides	28.1 ± 1.9^{a}	15.1 ± 0.4^{b}	-46.3	14.6 ± 0.9^{b}	-48.0
	Total	70.6 ± 4.5	70.6 ± 4.5	0.0	66.1 ± 5.8	-6.4
L71-920	Monosaccharides	48.6 ± 1.3^{a}	58.6 ± 1.0b	20.6	57.3 ± 1.7b	17.9
	Oligosaccharides	19.9 ± 1.3^{a}	10.6 ± 0.7^{b}	-46.7	11.6 ± 3.4^{b}	-41.7
	Total	68.4 ± 6.4	69.2 ± 4.5	1.2	68.9 ± 6.3	0.7

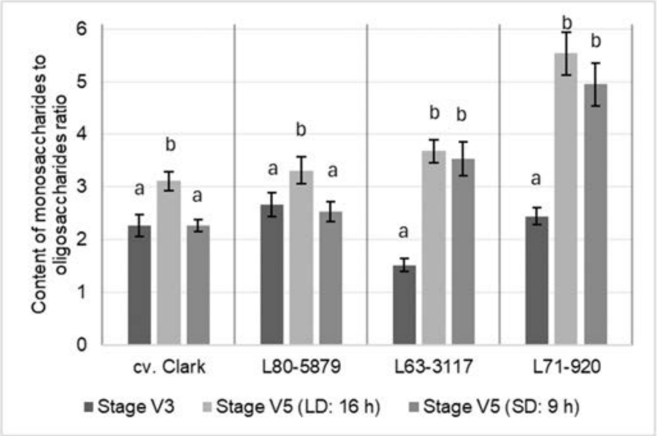
Note: Δ V5 (LD) vs. V3 – the percentage change in the parameter at stage V5 under long-day conditions relative to stage V3; Δ V5 (SD) vs. V3 – the percentage change in the parameter at stage V5 under short-day conditions relative to stage V3.

Comparisons were made within each isogenic soybean line between developmental stages V3 and V5 under different photoperiodic conditions. Different letters indicate statistically significant differences between values within the same row for each parameter, according to Tukey's post hoc test ($P<0.05$). The absence of letters indicates no statistically significant differences ($P>0.05$).

The content of oligosaccharides at the V3 stage was the highest in the cv. Clark and the L63-3117 line, which possess the recessive *e1* allele and the dominant *E3* allele, may indicate the influence of phytochromes on carbohydrate metabolism (Table 3).

Exposure to a long natural day led to a significant decrease in oligosaccharide content in the day-neutral isolines L63-3117 and L71-920, by 46.3% and 46.7% compared to the V3 stage, respectively, and in the short-day variety Clark, by 25%. The short-day line L80-5879, which carries the dominant *E1* allele in its genotype, did not show significant changes in the amount of oligosaccharides during the V3–V5 developmental period under long-day conditions. A more specific dynamic of oligosaccharide content was observed under short-day conditions. So, the day-neutral lines L63-3117 and L71-920, similar to the long-day treatment, demonstrated a significant decrease in the indicator during the V3–V5 period (by 48% and 42%, respectively), while the short-day lines did not show any significant changes.

Oligosaccharides and monosaccharides play an important role in various physiological processes, including osmotic balance, and serve as the starting material for polysaccharide synthesis. A high content of these carbohydrates may also indicate the plant's ability to better cope with stressful conditions such as drought, cold, or reduced light availability during the daily cycle (Blumstein et al., 2024). The ratio of monosaccharides to oligosaccharides is an important indicator of the plant's metabolic status, which reflects its physiological condition, response to stress factors, and the efficiency of photosynthetic and transport processes. At the V3 stage (start of the experiment), the monosaccharide-to-oligosaccharide ratio in all genotypes was approximately the same and ranged from 2.3 to 2.7, except for the isoline L63-3117, which has the dominant *E3* allele in its genotype and had the lowest ratio – 1.5 (Figure 2).



Note: comparisons were made within each isogenic soybean line between developmental stages V3 and V5 in different photoperiodic conditions (LD/SD); different letters indicate values that differed reliably from one another within one block, according to the results of comparison using the Tukey test ($P<0.05$).

Figure 2. Ratio of monosaccharide to oligosaccharide content in the leaves of soybean NILs under different photoperiod conditions

Throughout the experiment, the ratio of monosaccharides to oligosaccharides in the leaves of all studied soybean isolines changed depending on photoperiod duration and the genotype of the isoline (Figure 2). Under long-day conditions (16 h), this ratio increased in all tested plants, especially in isolines L63-3117 and L71-920, by 142% and 127% relative to the values at stage V3, respectively. The highest ratio at stage V5 under these conditions was observed in isoline L71-920, which has recessive alleles *e1*, *e2* and *e3* in its genotype. Under short-day conditions (9 h), the ratio of monosaccharides to oligosaccharides in the leaves of short-day lines (cv. Clark and L80-5879) at stage V5 did not change significantly compared to stage V3. In contrast, neutral-day lines (L63-3117 and L71-920) showed a similarly strong increase in this ratio as under long-day conditions. Comparison of the values revealed that at stage V5 in short-day lines grown under short-day conditions, the absence of significant changes in the parameter between stages V3 and V5 resulted in a significant decrease of the monosaccharide-to-oligosaccharide ratio compared to plants grown under long-day conditions. Meanwhile, in neutral-day lines, no significant differences in this ratio were observed between short- and long-day conditions at stage V5.

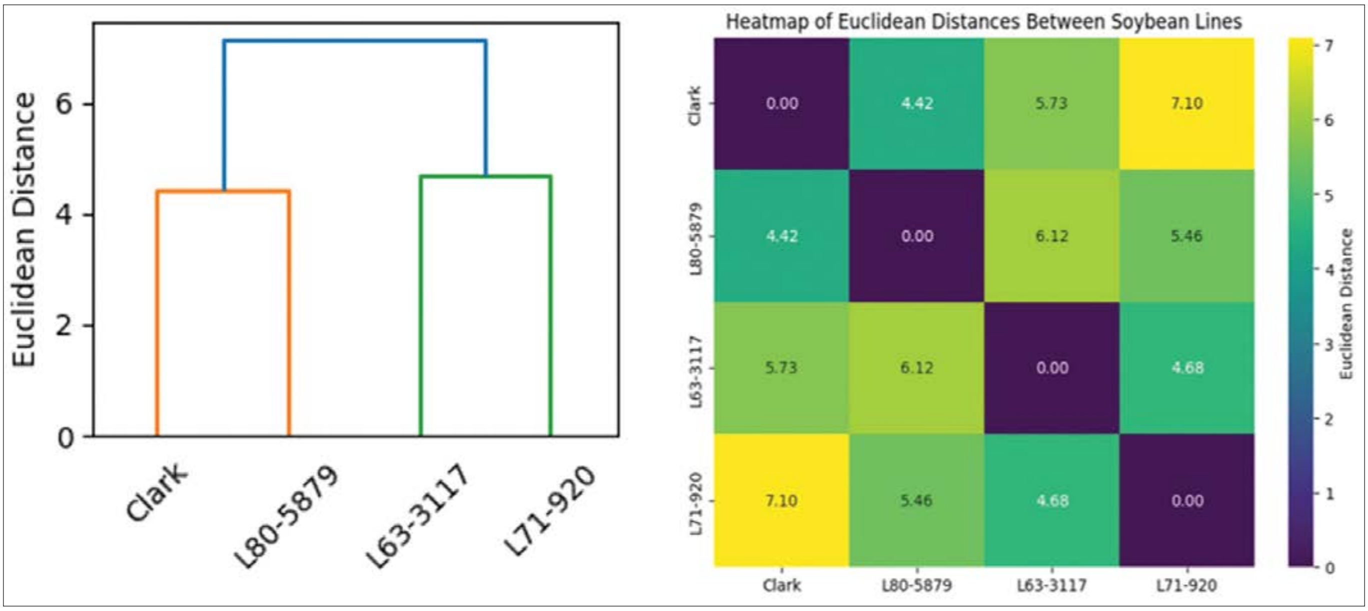
Despite some differences in the accumulation of monosaccharide and oligosaccharide fractions, the total content of soluble non-structural carbohydrates did not significantly change during the V3–V5 period, regardless of photoperiod treatment or isoline genotype (Table 3).

Classification of soybean NILs into photoperiodic groups using growth and biochemical traits

To analyze the response of plants to changes in day length during the V3–V5 developmental period, the relative changes (Δ) in metabolic and physiological traits (a total of 12 parameters) at stage V5 compared to stage V3 were calculated and expressed as percentages.

A K-means cluster analysis was performed, dividing the NILs into two groups: short-day plants (SDP) and neutral-day plants (NDP). Based on the Euclidean distances between lines, they were grouped according to their theoretical photoperiodic response under the climatic conditions of Ukraine: SDP – cv. Clark and L80-5879; NDP – L63-3117 and L71-920. This classification is supported by the duration of the vegetative growth phase observed in the experiment, which is a key parameter in determining the photoperiodic reaction of a plant (Table 2). Thus, the SDP and NDP groups differ not only in flowering time but also in growth dynamics and carbohydrate metabolism during the V3–V5 developmental period (Figure 3).

However, to evaluate the interaction between genotype and photoperiod and their influence on growth and soluble carbohydrate content at the V5 stage, it is more appropriate to use the measured values of the traits obtained under short- and long-day conditions, as they represent the outcome of photoperiodic effects during the V3–V5 period.



Note: The heat map shows the Euclidean distance between the soybean isolines.

Figure 3. Hierarchical clustering of soybean isolines by photoperiodic response, considering the change in the value of indicators of metabolic and physiological state of the line (12 traits) from the V5 developmental phase to the V3 phase at different day lengths

When these experimentally obtained values are considered, the clustering of the lines differs. For instance, the short-day cultivar Clark shows the smallest Euclidean distance (3.40) from the neutral-day line L63-3117 (Figure 4). At the same time, the Euclidean distance between L63-3117 and the other lines is greater than that between it and Clark. This is likely due to the presence of the dominant *E3* allele in both Clark and L63-3117. Thus, based on clustering that takes into account the empirical values of metabolic and growth traits obtained under different photoperiod conditions, the lines were grouped as follows: SDP – Clark, L80-5879, and L63-3117; NDP – L71-920.

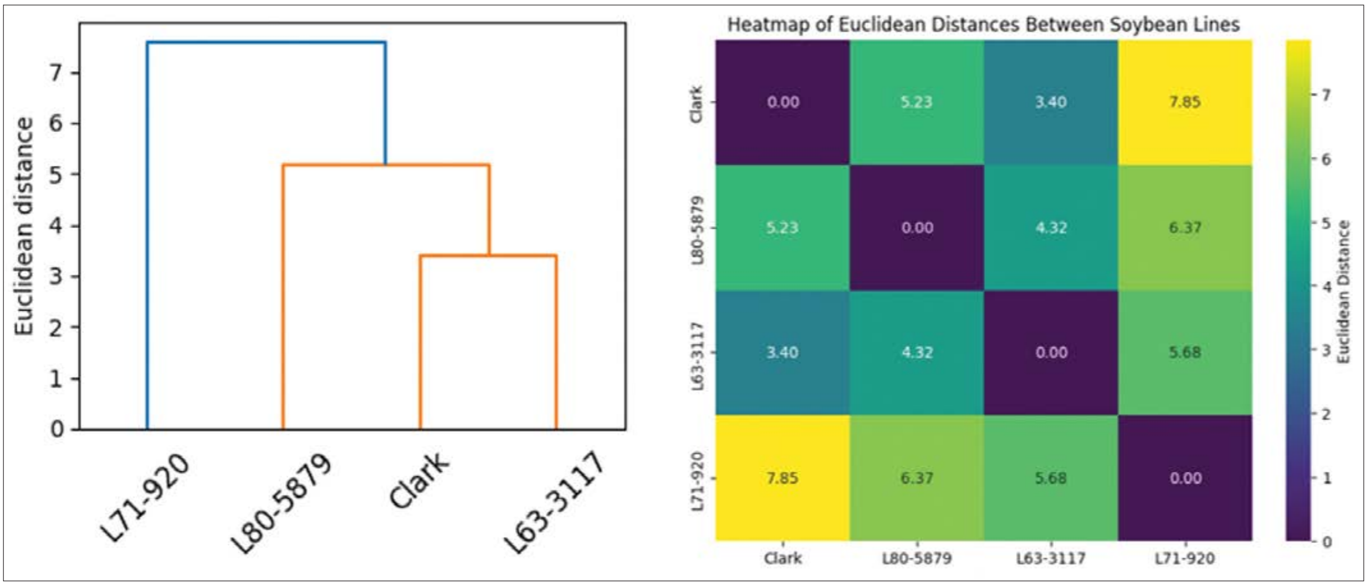


Figure 4. Hierarchical clustering of soybean isolines by photoperiodic response, based on standardized actual values of soybean NILs in the V5 development phase under different day lengths

Besides the *E3* allele, the genotype of the L63-3117 line, as well as all others, contains the dominant *E4* allele. It is known that the combined activity of the expression products of the *E3* and *E4* genes causes a delay in flowering under day lengths of 20 hours or more. That is, this isoline is neither absolutely short-day nor neutral-day and has a wide reaction norm in photoperiod sensitivity. That is why the profile of standardized values of growth and biochemical indicators of the Clark cultivar and the L63-3117 line on the heatmap is similar (especially for indicators under long-day conditions), even though under the climatic conditions of Ukraine, L63-3117 is classified as a neutral-day plant, which is confirmed by phenological observations (Figure 5; Table 2). That is, L63-3117 shows a neutral-day reaction in the duration of the vegetative phase, but because of the activity of the *E3* allele, its metabolic and growth profiles under long days are similar to the short-day cv. Clark.

Influence of E-genes on growth and biochemical parameters

It is known that the expression of genes *E1*, *E2*, and *E3* is enhanced under long-day conditions. For the analysis of the effect of E genes on growth and biochemical parameters, the percentage difference of these parameters at the V5 developmental stage under long-day conditions relative to short-day conditions was compared (Table 4).

Using these calculations, a correlation analysis was performed, based on which the influence of the *E1* and *E2* alleles on growth parameters and carbohydrate content was identified. It was determined that the *E2* allele under long-day conditions strongly correlates with growth parameters (RGR: $\rho = 0.88$, $P<0.05$; NAR: $\rho = 0.80$, $P<0.05$) and negatively correlates with the content of oligosaccharides ($\rho = -0.87$, $P<0.05$). Thus, according to the analysis, the dominant *E2* allele plays an important role in increasing vegetative growth under long-day conditions, which was observed for the cv. Clark. It is likely that under long-day conditions, with prolonged vegetative growth caused by *E2*, the carbohydrate flow is directed to actively growing organs (apical meristems, young leaves). For this reason, the content of oligosaccharides (the transport form of carbohydrates) in the leaves significantly decreases under long-day conditions. Meanwhile, considering the NAR parameter and the increased content of monosaccharides, the photosynthetic activity of the cv. Clark, which carries the dominant *E2* allele in its genotype, is also increased under long-day conditions.

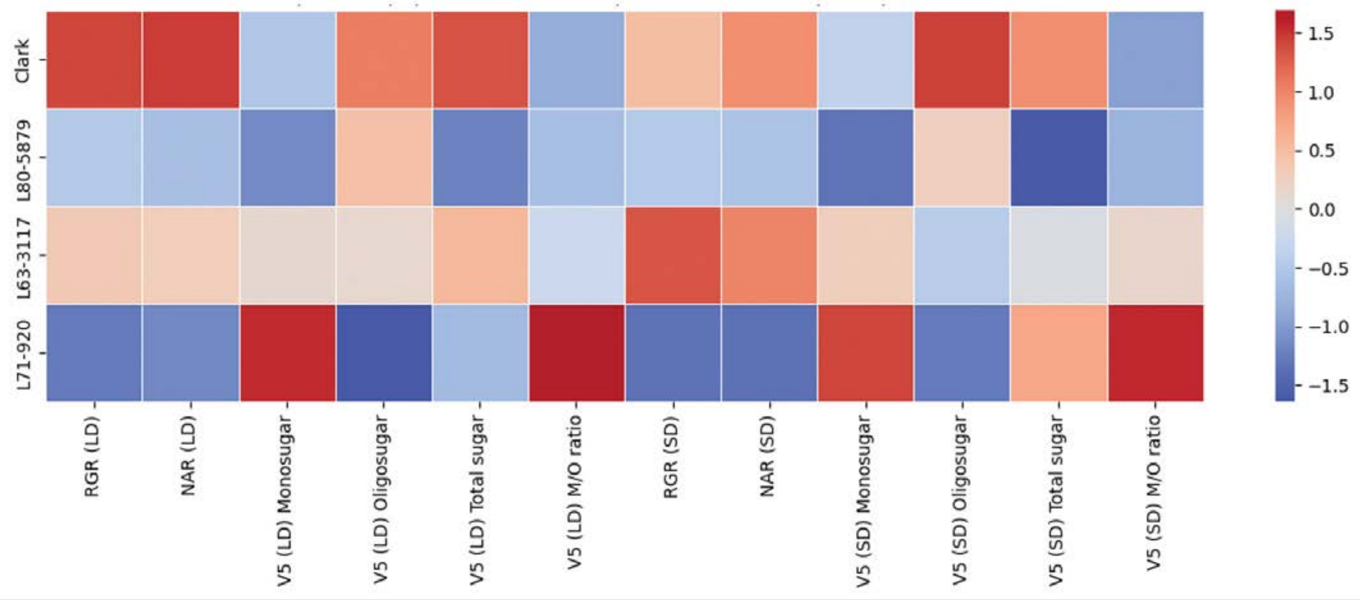


Figure 5. Heatmap of standardized values of growth and metabolic parameters under long- and short-day conditions at the V5 developmental stage

Table 4. Percentage differences in growth and carbohydrate content parameters under long-day (LD, 16 h) compared to short-day (SD, 9 h) conditions for soybean isolines in V5 developmental stages (%)

Isoline	Monosugars	Oligosugars	Total sugars	Mono/Oligo ratio	RGR	NAR
Clark	12.0	−18.3	2.7	37.0	148.5	125.5
L80-5879	21.7	−7.0	13.6	30.8	81.7	72.2
L63-3117	7.8	3.4	6.8	4.3	36.3	47.2
L71-920	2.7	-8.6	0.4	11.9	90.4	91.2

Previously, for the cv. Clark under long-day conditions, an increase in photosynthetic pigment content was observed, which complements the obtained results (Yukhno et al., 2024).

For the *E1* allele, under long-day conditions, insignificant correlation coefficients with growth parameters were determined (RGR: ρ = -0.23, *P*>0.05; NAR: ρ = -0.28, *P*>0.05), but for the line L80-5879 under long-day conditions, an increase in these parameters was observed. Thus, the cause of changes in the parameters under long-day conditions is not the *E1*. This is logical because, unlike other alleles, the *E1* is not a component of the plant photoreceptor system (*E3*, which encodes phytochrome A) or the circadian system (*E2*, a regulator of circadian clock genes), which are capable of direct regulation of processes depending on photoperiod perception. The *E1* – although, according to literature data, it shows enhanced expression under long-day conditions – depends on the functioning of the plant photoreceptor system. However, under long-day conditions, the *E1* allele demonstrates a significant positive correlation with monosaccharide content (ρ = 0.92, *P*<0.05) and no significant correlation with oligosaccharide content (ρ = -0.21, *P*>0.05). *E1* allele likely promotes an increased photosynthetic activity during the extended vegetative phase under long-day conditions; however, since it does not affect the distribution of assimilates – a factor that directly influences RGR – it consequently does not impact RGR. Also, under long-day conditions, an increase in photosynthetic pigment content was previously determined in the leaves of the L80-5879 line, which has the *E1* allele, potentially ensuring a sufficient level of assimilation processes (Yukhno et al., 2024).

The *E3* allele demonstrates a moderate positive correlation with growth and assimilation parameters (RGR: ρ = 0.65, *P*<0.05; NAR: ρ = 0.62, *P*<0.05), which is supported by actual measurements – specifically, the increase in these traits under long-day conditions in the L63-3117 line. At the same time, *E3* shows no correlation with the content of mono- or oligosaccharides, indicating that it does not significantly affect their levels under long-day compared to short-day conditions. Interestingly, another photoperiod-insensitive isoline, L71-920, which carries recessive alleles *e1*, *e2* and *e3*, demonstrates similar trends. This suggests that photoperiod-insensitive lines may show higher stability in response to varying photoperiods.

CONCLUSION

The study revealed different adaptive strategies of short-day (SD) and neutral-day (LD) soybean isogenic lines in response to varying photoperiodic conditions, mediated by the combination of *E* alleles. Short-day lines (cv. Clark and L80-5879) demonstrated a strong dependence on day duration. Under long-day conditions (16 h), these isolines showed higher relative growth rates (RGR) and net assimilation rates (NAR), which were caused by increased photosynthetic activity, especially in the cv. Clark, which has the recessive *e1* allele along with the dominant *E2* and *E3* alleles. This suggests an adaptive strategy involving the preferential accumulation of vegetative biomass under long-day conditions, likely aimed at maximizing resource uptake before transitioning to flowering. However, under short-day conditions (9 h), the SD lines demonstrated a significant decrease in RGR (up to 60% in cv. Clark) and NAR, as well as a decrease in monosaccharide content, indicating a shift in resource allocation toward reproductive development, which corresponds to their short-day response. The alleles at the *E1* and *E2* loci play an important role in mediating these responses. Specifically, *E1* promotes enhanced photosynthetic activity through the accumulation of photosynthetic pigments, leading to increased levels of monosaccharides, while *E2* synchronizes photosynthesis with circadian rhythms, facilitating more efficient light utilization under long-day conditions, thereby increasing photosynthetic productivity and growth.

At the same time, neutral-day (ND) isolines (L63-3117 and L71-920) demonstrated higher stability of growth and metabolic parameters under different photoperiods, reflecting a more flexible adaptive strategy. These isolines, particularly L63-3117 carrying the dominant *E3* allele, maintained relatively high RGR and NAR under short-day conditions, with minimal differences compared to long-day conditions.

Such stability is likely due to the recessive state of the *e1*, *e2*, and – in the case of L71-920 – *e3* alleles, which reduce repression of the flowering inducer *GmFT2a*, allowing early flowering and sustained vegetative growth under both long- and short-day conditions. Notably, the L63-3117-line increased monosaccharide content under short-day conditions (by up to 21.2%) at the V5 stage compared to the V3 stage, indicating an adaptive mechanism for maintaining metabolic activity and growth under limited light availability. The ratio of monosaccharides to oligosaccharides significantly increased in ND isolines under both photoperiods, indicating efficient carbohydrate mobilization to support both vegetative and reproductive processes.

Cluster analysis based on actual parameters at the V5 developmental stage under different photoperiods further showed that the presence of the dominant *E3* allele in L63-3117 results in metabolic and growth profiles that are more similar to those of the cv. Clark under long-day conditions, despite its classification as a neutral-day isoline based on vegetative phase duration. This indicates a unique photoperiodic response, in which *E3* enhances photosynthetic efficiency and biomass accumulation under long-day conditions, similarly to the strategies of short-day responsive lines, while maintaining the metabolic stability characteristic of ND isolines under short-day conditions.

In summary, SD isolines adopt a strategy of maximizing vegetative growth under long-day conditions and reallocating resources to reproduction under short-day conditions, whereas ND isolines demonstrate metabolic and growth stability, allowing them to effectively adapt to different photoperiodic conditions. From a practical perspective, the results highlight the importance of considering allelic combinations at *E-series* maturity loci when selecting soybean genotypes for specific photoperiodic environments. The observed differences in growth dynamics and carbohydrate metabolism among isolines with contrasting allelic backgrounds suggest that these traits may serve as physiological markers for assessing photoperiod adaptability. They may contribute to the development of soybean cultivars with improved growth stability under changing climatic conditions and variable photoperiod.

REFERENCES

Ali, W., Ahmad, M., Iftikhar, F., Qureshi, M. S. (2020) Nutritive potentials of soybean and its significance for human health and animal production: A review. Eurasian Journal of Food Science and Technology, 4 (1), 41-53. Available at: https://dergipark.org.tr/en/download/article-file/1273470 [Accessed 13 March 2025].

Blumstein, M., Oseguera, M., Caso-McHugh, T., Des Marais, D. L. (2024) Nonstructural carbohydrate dynamics' relationship to leaf development under varying environments. New Phytologist, 241, 102-113. DOI: https://doi.org/10.1111/nph.19333

Cao, D., Takeshima, R., Zhao, C., Liu, B., Jun, A., Kong, F. (2017) Molecular mechanisms of flowering under long days and stem growth habit in soybean. Journal of Experimental Botany, 68 (8), 1873-1884. DOI: https://doi.org/10.1093/jxb/erw394

Cho, L. H., Pasriga, R., Yoon, J., Kim, J. (2018) Roles of sugars in controlling flowering time. Journal of Plant Biology, 61, 121-130. DOI: https://doi.org/10.1007/s12374-018-0081-z

Cober, E. R., Curtis, D. F., Stewart, D. W., Morrison, M. J. (2014) Quantifying the effects of photoperiod, temperature and daily irradiance on flowering time of soybean isolines. Plants, 3 (4), 476-497. DOI: https://doi.org/10.3390/plants3040476

Dogra, A. K., Kaur, J., Srivastava, A. K. (2015) Relationship between growth and photosynthetic efficiency of soybean (*Glycine max* L. Merrill) genotypes under variable photoperiods. Vegetos, 28, 183-193. DOI: https://doi.org/10.5958/2229-4473.2015.00054.3

Dissanayaka, A., Rodriguez, T. O., Di, S., Yan, F., Githiri, S. M., Rodas, F. R., Abe, J., Takahashi, R. (2016) Quantitative trait locus mapping of soybean maturity gene E5. Breeding Science, 66 (3), 407-415. DOI: https://doi.org/10.1270/jsbbs.15160

FAO (2024) FAOSTAT database. Food and Agriculture Organization of the United Nations. Available at: http://fao.org/faostat/en/ [Accessed 20 March 2025].

Gupta, S., Kumawat, G., Agrawal, N., Tripathi, R., Rajesh, V., Nataraj, V., Maranna, S., Satpute, G. K., Chandra, S., Ratnaparkhe, M. B., Srivastava, M. K., Khandekar, N., Jain, M. (2022) Photoperiod trait: Insight in molecular mechanism for growth and maturity adaptation of soybean (*Glycine max*) to different latitudes. Plant Breeding, 141 (4), 483-500. DOI: https://doi.org/10.1111/pbr.13041

Hlushach, D. V., Avksentieva, O. O. (2024) Influence of Bradyrhizobium japonicum on the growth parameters and formation of the assimilation apparatus in *E*-gene isogenic lines of soybean. Regulatory Mechanisms in Biosystems, 15 (1), 131-141. DOI: https://doi.org/10.15421/022420

Hunt, R. (2017) Growth analysis, individual plants. In: Thomas, B., Murray, B. G., Murphy, D. J., eds. Encyclopedia of Applied Plant Sciences. Oxford: Academic Press, 421-429. DOI: https://doi.org/10.1016/B978-0-12-394807-6.00226-4

Hussain, S., Iqbal, N., Rahman, T., Liu, T., Brestic, M., Safdar, M. E., Asghar, M. A., Farooq, M. U., Shafiq, I., Ali, A., Shoaib, M., Chen, G., Qin, S., Liu, W., Yang, W. (2019) Shade effect on carbohydrates dynamics and stem strength of soybean genotypes. Environmental and Experimental Botany, 162, 374-382. DOI: https://doi.org/10.1016/j.envexpbot.2019.03.011

Hussain, S., Pang, T., Iqbal, N., Shafiq, I., Skalický, M., Brestič, M., Safdar, M. E., Mumtaz, M., Ahmad, A., Asghar, M. A., Raza, A., Allakhverdiev, S. I., Wang, Y., Wang, X. C., Yang, F., Yong, T., Liu, W., Yang, W. (2020) Acclimation strategy and plasticity of different soybean genotypes in intercropping. Functional Plant Biology, 47 (7), 592-610. DOI: https://doi.org/10.1071/FP19161

Kong, F., Nan, H., Cao, D., Li, Y., Wu, F., Wang, J., Lu, S., Yuan, X., Cober, E. R., Abe, J., Liu, B. (2014) A new dominant gene *E9* conditions early flowering and maturity in soybean. Crop Science, 54 (6), 2529-2535. DOI: https://doi.org/10.2135/cropsci2014.03.0228

Kumudini, S. (2002) Trials and tribulations: A review of the role of assimilate supply in soybean genetic yield improvement. Field Crops Research, 75, 211-222. DOI: https://doi.org/10.1016/S0378-4290(02)00027-8

Lamont, B. B., Williams, M. R., He, T. (2023) Relative growth rate (RGR) and other confounded variables: Mathematical problems and biological solutions. Annals of Botany, 131 (4), 555-568. DOI: https://doi.org/10.1093/aob/mcad031

Li, X., Schmid, B., Wang, F., Paine, C. E. T. (2016) Net assimilation rate determines the growth rates of 14 species of subtropical forest trees. PLOS ONE, 11 (3), e0150644. DOI: https://doi.org/10.1371/journal.pone.0150644

Li, Y., Hou, Z., Li, W., Li, H., Lu, S., Gan, Z., Du, H., Li, T., Zhang, Y., Kong, F., Cheng, Y., He, M., Ma, L., Liao, C., Li, Y., Dong, L., Liu, B., Cheng, Q. (2021) The legume-specific transcription factor *E1* controls leaf morphology in soybean. BMC Plant Biology, 21 (1), 531. DOI: https://doi.org/10.1186/s12870-021-03301-1

Lu, Q., Zhao, L., Li, D., Hao, D., Zhan, Y., Li, W. (2014) A GmRAV ortholog is involved in photoperiod and sucrose control of flowering time in soybean. PLOS ONE, 9 (2), e89145. DOI: https://doi.org/10.1371/journal.pone.0089145

Luo, X., Yin, M., He, Y. (2021) Molecular genetic understanding of photoperiodic regulation of flowering time in Arabidopsis and soybean. International Journal of Molecular Sciences, 23 (1), 466. DOI: https://doi.org/10.3390/ijms23010466

Miranda, C., Scaboo, A., Cober, E., Denwar, N., Bilyeu, K. (2020) The effects and interaction of soybean maturity gene alleles controlling flowering time, maturity, and adaptation in tropical environments. BMC Plant Biology, 20, 65. DOI: https://doi.org/10.1186/s12870-020-2276-y

Ort, N. W., Morrison, M. J., Cober, E. R., Samanfar, B., Lawley, Y. E. (2022) Photoperiod affects node appearance rate and flowering in early maturing soybean. Plants, 11 (7), 871. DOI: https://doi.org/10.3390/plants11070871

Osnato, M., Cota, I., Nebhnani, P., Cereijo, U., Pelaz, S. (2022) Photoperiod control of plant growth: flowering time genes beyond flowering. Frontiers in Plant Science, 12, 805635. DOI: https://doi.org/10.3389/fpls.2021.805635

Porro, M., Viti, S., Antoni, G., Neri, P. (1981) Modifications of the Park-Johnson ferricyanide submicromethod for the assay of reducing groups in carbohydrates. Analytical Biochemistry, 118 (2), 301-306. DOI: https://doi.org/10.1016/0003-2697(81)90586-8

Raievska, I., Schogolev, A. (2024) Genes of photoperiod sensitivity and early maturity *E1-E4*: dynamics of soybean growth in different daylength conditions. Studia Biologica, 18 (3), 87-97. DOI: https://doi.org/10.30970/sbi.1803.784

Sachin, Ashvathama, V. H., Naidu, G. K., Kiran, B. O. (2024) Using biochemical and growth parameters to assess soybean yield potential. Journal of Experimental Agriculture International, 46 (9), 105-110. DOI: https://doi.org/10.9734/jeai/2024/v46i92809

Shipley, B. (2006) Net assimilation rate, specific leaf area and leaf mass ratio: which is most closely correlated with relative growth rate? A meta-analysis. Functional Ecology, 20, 565-574. DOI: https://doi.org/10.1111/j.1365-2435.2006.01135.x

Staniak, M., Szpunar-Krok, E., Kocira, A. (2023) Responses of soybean to selected abiotic stresses – photoperiod, temperature and water. Agriculture, 13 (1), 146. DOI: https://doi.org/10.3390/agriculture13010146

Sun, Z., Yuan, L., Wang, Y., Fang, R., Lin, X., Li, H., Chen, L., Wu, Y., Huang, X., Kong, F., Liu, B., Lu, S., Kong, L. (2024) Post-flowering photoperiod sensitivity of soybean in pod-setting responses. Biology, 13 (11), 868. DOI: https://doi.org/10.3390/biology13110868

Taniguchi, T., Murayama, N., Ario, N., Nakagawa, A. C. S., Tanaka, S., Tomoita, Y., Hasegawa, M., Hamaoka, N., Iwaya-Inoue, M., Ishibashi, Y. (2020) Photoperiod sensing of leaf regulates pod setting in soybean (*Glycine max* (L.) Merr.). Plant Production Science, 23 (3), 360-365. DOI: https://doi.org/10.1080/1343943x.2019.1709512

Tasma, I. M., Shoemaker, R. C. (2003) Mapping flowering time gene homologs in soybean and their association with maturity loci. Crop Science, 43 (1), 319-328. DOI: https://doi.org/10.2135/cropsci2003.3190

Wang, C., Liu, X., Hao, X., Pan, Y., Zong, C., Zeng, W., Wang, W., Xing, G., He, J., Gai, J. (2022) Evolutionary variation of accumulative day length and accumulative active temperature required for growth periods in global soybeans. Agronomy, 12 (4), 962. DOI: https://doi.org/10.3390/agronomy12040962

Wang, Q., Liu, W., Leung, C. C., Tartè, D. A., Gendron, J. M. (2023) Parallel mechanisms detect different photoperiods to independently control seasonal flowering and growth in plants. bioRxiv. DOI: https://doi.org/10.1101/2023.02.10.528016

Yukhno, Y. Y., Avksentieva, O. O., Glushach, D. (2024) Formation and functioning of the assimilation apparatus of soybean lines isogenic for E genes under different photoperiod durations. Bulletin of Sumy National Agrarian University. The Series: Agronomy and Biology, 56 (2), 103-111. DOI: https://doi.org/10.32782/agrobio.2024.2.13

Zhai, H., Wan, Z., Jiao, S., Zhou, J., Xu, K., Nan, H., Liu, Y., Xiong, S., Fan, R., Zhu, J., Jiang, W., Pang, T., Luo, X., Wu, H., Yang, G., Bai, X., Kong, F., Xia, Z. (2022) GmMDE genes bridge the maturity gene *E1* and florigens in photoperiodic regulation of flowering in soybean. Plant Physiology, 189 (2), 1021-1036.
DOI: https://doi.org/10.1093/plphys/kiac092

Zhang, X., Wu, T., Wen, H., Song, W., Xu, C., Han, T., Sun, S., Wu, C. (2021) Allelic variation of soybean maturity genes *E1–E4* in the Huang-Huai-Hai River Valley and the Northwest China. Agriculture, 11 (6), 478. DOI: https://doi.org/10.3390/agriculture11060478

Zhmurko, V. V., Al-Hamadeni, H. N. H. (2019) The effect of photoperiod duration on the dynamics of content of water-soluble carbohydrates in soybean seeds (*Glycine max* (L.) Merr.). Science and Education a New Dimension. Natural and Technical Sciences, VII (23), 25-28. DOI: https://doi.org/10.31174/send-nt2019-193vii23-05