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THE IMPACT OF ALLELIC VARIATION IN *E*-GENES ON TOTAL PHENOLIC CONTENT AND FLAVONOID ACCUMULATION IN SOYBEAN (*GLYCINE MAX* (L.) MERR.) SEEDS

Aim. To investigate the impact of early-stage photoperiodic induction (V3–V5 stages) n the partitioning of phenolic compounds and flavonoids in mature seeds of soybean near-isogenic lines (NILs) carrying various maturity gene combinations (*E1*–*E3*). ***Methods.*** Nearly isogenic lines (NILs) of soybean, in which the *E*-genes are located at different allelic loci, were used. Short-day (ShD) lines – genotypes *E1E2E3, E1e2e3* and neutral-day (ND) lines – genotypes *e1E2e3, e1e2E3, e1e2e3*. Starting from the V3 stage, plants were exposed to either a natural long day (16 h) or an inductive short day (9 h) for 14 days. Total phenolic content (TPC) and flavonoid accumulation were subsequently analyzed in mature seeds. ***Results.*** A profound "metabolic memory" effect was observed, where early induction determines the final seed metabolome. ShD lines (with *E1*) exhibited significantly higher TPC, particularly following the 9-hour induction. In contrast, ND lines showed lower TPC but a significant shift toward flavonoid biosynthesis. The triple-recessive *e1e2e3* genotype achieved the highest flavonoid content and a four-fold increase in the flavonoid-to-phenolic ratio compared to the dominant *E1E2E3* line. The *e1E2e3* genotype demonstrated metabolic stability, maintaining a constant flavonoid share regardless of the initial photoperiod. ***Conclusions.*** *E*-genes act as metabolic gatekeepers: dominant alleles prioritize generalized phenolic accumulation, while recessive alleles trigger specialized flavonoid partitioning. Photoperiodic neutrality is genetically linked to an enriched flavonoid profile in soybean seeds.

Keywords: soybean (*Glycine max* (L.) Merr.) seeds, isogenic lines, *E*-genes, photoperiod, flavonoids, phenolic compounds.

Soybean (*Glycine max* (L.) Merr.) is one of the most economically significant crops globally, serving as a primary source of vegetable protein and oil, as well as a rich reservoir of bioactive secondary metabolites (Ali et al., 2020). Among these, phenolic compounds, particularly flavonoids, play a dual role: they are essential for plant adaptation to environmental stresses – such as UV radiation and pathogen defense – and provide significant health benefits for human nutrition due to their antioxidant, estrogenic, and anticancer properties (Corso et al., 2020, Dixon and Pasinetti, 2010).

The growth, development, and metabolic profile of soybean are fundamentally governed by its response to photoperiod (Zhang, 1997). As a short-day plant, soybean utilizes a complex genetic network to perceive day length and trigger the transition from vegetative to reproductive stages (Lin et al., 2021). This photoperiodic control is primarily mediated by the "maturity genes" (the *E* series) (Lin et al., 2021). While several loci have been identified, including the more recently discovered *E9* and *E10* which modulate flowering time through the fine-tuning of florigen expression, and the *J* locus, which facilitates the "long juvenile period" allowing soybean cultivation in tropical short-day environments, the *E1*, *E2*, and *E3* loci remains the most critical regulators of development in temperate latitudes (Lin et al., 2021, Jiang et al., 2014).

The molecular signaling cascade is centered on the regulation of *GmFT* (*Flowering Locus T*) genes, which are the primary targets of the *E* gene network (Lin et al., 2021). Dominant *E* alleles act as repressors that inhibit the expression of *GmFT2a* and *GmFT5a*, thereby delaying the floral transition (Cao et al., 2017). Within this hierarchy, *E1* is the most potent repressor, encoding a legume-specific B3-domain protein (Lin et al., 2021). *E2* functions as an ortholog of *GIGANTEA* (*GI*), linking the circadian clock to developmental timing, while *E3* encodes a phytochrome A photoreceptor (*GmPHYA3*) responsible for sensing light quality and stabilizing the *E1* suppressor under long-day conditions (Xu et al., 2013).

The interaction of *E1*, *E2*, and *E3* forms the genetic backbone for most commercial cultivars in temperate regions (Jiang et al., 2014). Crucially, their influence on the duration of the vegetative phase and the timing of maturation directly correlates with the "metabolic window" available for the phenylpropanoid pathway. This makes these maturity genes indirect yet powerful regulators of the seed phenolic complex (Zhu et al., 2018). Recent evidence suggests that the signaling crosstalk between light-sensing receptors and downstream transcriptional factors does more than time the harvest; it orchestrates a systemic shift in the partitioning of secondary metabolites (Corso et al., 2020).

Despite the extensive characterization of *E* genes in relation to phenology, their specific impact on the partitioning of phenolic compounds in seeds – particularly how different allelic combinations affect the ratio of flavonoids to total phenolics – remains insufficiently explored (Josipović et al., 2016, Malenčić et al., 2012). Understanding this relationship is crucial for "precision breeding" of soybean cultivars with optimized phytochemical profiles.

This study aims to evaluate the total phenolic content (TPC), flavonoid accumulation, and their relative proportions in the seeds of unique near-isogenic lines (NILs). By analyzing these lines under long-day (16 h) and short-day (9 h) conditions, we seek to elucidate how the genetic status of *E1*, *E2*, and *E3* modulates the seed phenolic metabolome, providing new insights into the biochemical pleiotropy of soybean maturity genes.

Materials and methods

Plant materials. As plant material in this study, four genotypes were used – the cultivar Clark and near-isogenic lines (NILs) of soybean (*G. max*) developed within the genetic background of this cultivar. The isolines differ in the allelic state of *E*-genes (Lin et al., 2021), which determine the photoperiodic response and the maturity period after flowering. 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) (Yuhno and Zhmurko, 2010). The NIL seeds used in the research were provided by National Center for Plant Genetic Resources of Ukraine, Kharkiv. *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 leached heavy loamy chernozem. No fertilizers or bacterial preparations were applied to the plants. Sowing was performed manually on plots of 1 m², 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). After this all plants were grown again under long-day conditions until the end of the growing season. *Extraction procedure*. Plant material (1 g of whole seeds per sample) was ground in a mill, reduced to a fine powder, and extracted with 70% aqueous acetone (50 mL) for 20 minutes. The extracts were rapidly vacuum-filtered through a sintered glass funnel and kept refrigerated before assay. *Determination of total polyphenol contents.* Total polyphenols were determined by the Folin–Ciocalteu method (Kroyer, 2003). The amount of total polyphenols was calculated as a gallic acid equivalent (GAE) from the calibration curve of gallic acid standard solutions (covering the concentration range between 0.1 and 1.0 mg/mL) and expressed as milligrams of GAE per gram of dry weight (DW). *Determination of flavonoids.* Total flavonoids were determined after extraction of plant material (1 g of whole seeds) with 20mL of extracting solvent methanol–water–acetic acid (140 : 50 : 10 by volume), for 60 minutes, according to the procedure of Marckam (Marckam, 1989). The amount of flavonoids was calculated as a rutin equivalent (RE) from the calibration curve of rutin standard solutions and expressed as milligrams of RE per gram of DW. All measurements were done in triplicate. *Statistical analysis.* Statistical analysis was performed using one-way and two-way analysis of variance (ANOVA), followed by Tukey's HSD test ($p < 0.05$) to determine significant differences between genotypes and treatments. Data are presented

as means ± standard deviations (x ± SD) in figures and tables.

Results and discussion

Genotype-specific Response of Total Phenolic Content to Photoperiodic Shifts. The accumulation of total phenolic compounds (TPC) in soybean seeds demonstrated a clear dependence on the allelic state of the *E* genes and the photoperiodic conditions during the early vegetative stage. Our results show that even a brief (14-day) exposure to different photoperiods starting from the V3 stage significantly influences the final seed metabolome.

As shown in Fig. 1, the ShD-lines (*E1E2E3* and *E1e2e3*) exhibited the highest overall levels of TPC. In the triple-dominant genotype *E1E2E3*, the TPC reached its maximum at 18.09 mg/g under the 9-hour photoperiod. This suggests that the presence of the *E1* allele, which is a potent repressor of the floral transition, promotes a longer vegetative buildup, effectively "priming" the phenylpropanoid pathway for higher total phenolic output (Jiang et al., 2014).

Interestingly, the induction short-day (ShD) resulted in a significant increase in TPC for these sensitive genotypes compared to the natural 16-hour long-day (LD) conditions. This indicates that the 9-hour "pulse" at the vegetative stage was sufficient to trigger a metabolic shift that persists through the grain-filling period.

In contrast, the ND-lines, characterized by the recessive *e1* allele (*e1E2e3*, *e1e2E3*, and *e1e2e3*), showed significantly lower TPC levels and reduced sensitivity to the initial photoperiodic treatment. The genotype *e1E2e3* demonstrated remarkable stability, with TPC values remaining nearly constant (10.26 mg/g under LD vs. 9.59 mg/g under ShD). The triple-recessive genotype *e1e2e3* yielded the lowest TPC values (8.51–9.32 mg/g).

This disparity confirms that the *E1* locus is not only a developmental regulator but also a metabolic gatekeeper. In the absence of *E1* (recessive *e1*), the plant bypasses the prolonged vegetative regulatory phase, leading to a more "diluted" phenolic profile in the mature seeds (Lin et al., 2021).

The data suggest an additive effect of the *E2* and *E3* loci when *E1* is dominant. The decrease in TPC from *E1E2E3* to *E1e2e3* (from 18.09 to 13.79 mg/g under ShD) highlights that while *E1* is the primary driver, the *E2* (*GIGANTEA* ortholog) and *E3* (*Phytochrome A*) loci are essential for maximizing the flux through the phenolic biosynthetic pathway (Xu et al., 2013). The early 9-hour photoperiodic induction likely accelerates the development of sensitive lines (Yuhno and Zhmurko, 2010), but the presence of dominant *E* alleles ensures that this acceleration does not compromise the synthesis of secondary metabolites.

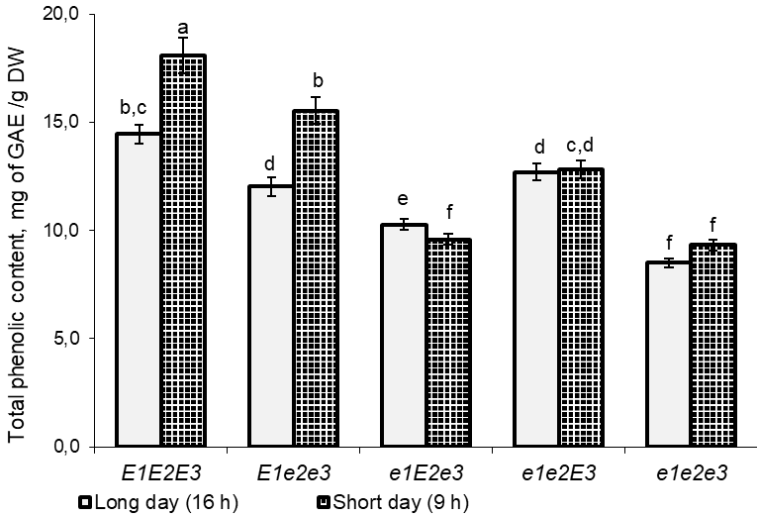

Fig. 1. Total phenolic content (TPC) in seeds of soybean isolines differing in *E* gene alleles under different photoperiodic treatments, mg of GAE /g DW (Long day – 16 h, Short day – 9 h; n = 10, x ± SD). Comparisons were made between different isolines and photoperiodic conditions. Different letters indicate statistically significant differences based on Tukey's post hoc test ($p < 0.05$).

Divergent Regulation of Flavonoid Accumulation and Metabolic Partitioning. The accumulation of flavonoids in soybean seeds, as observed in our study, does not follow the same quantitative logic as total phenolic content (TPC). While TPC is maximized in genotypes with dominant *E* alleles, the absolute and relative concentrations of flavonoids reach their peak in recessive, neutral-day lines. This phenomenon suggests a fundamental metabolic trade-off between the various branches of the phenylpropanoid pathway, orchestrated by the photoperiodic genetic clock (Lin et al., 2021, Josipović et al., 2016).

The data illustrated in Fig. 2 reveals a striking inverse correlation: the transition from the triple-dominant genotype *E1E2E3* to the triple-recessive *e1e2e3* results in a nearly 3-fold increase in absolute flavonoid content (from 0.32 to 0.92 mg/g).

From a biochemical perspective, all phenolic compounds share the same precursor – L-phenylalanine (Marckam, 1989). The commitment of this precursor to specific downstream products is regulated by "gatekeeper" enzymes (Corso et al., 2020). Our findings suggest that the E1 protein, either directly or through downstream florigen signaling (Lin et al., 2021), may prioritize the flux toward the monolignol branch (leading to lignin) or the synthesis of simpler phenolic acids. In contrast, the absence of *E1* (as seen in ND-lines) appears to "open" the gateway to the flavonoid branch, likely by increasing the expression or activity of Chalcone Synthase (CHS) and Chalcone Isomerase (CHI) (Corso et al., 2020, Malenčić et al., 2012).

The most revealing metric of this study is the Flavonoid-to-Total Phenolic ratio (Table). We observed a stepwise increase in this "partitioning index" linked to the loss of dominant maturity alleles. The "Dominant Strategy" (*E1E2E3*): flavonoids represent a mere 2.34–2.63% of the total phenolic pool. This suggests a "quantity-over-specificity" strategy, where the plant, sensitive to the 9-hour photoperiodic pulse, rapidly accumulates a broad spectrum of phenolics, possibly for structural reinforcement or general stress protection (Dixon and Pasinetti, 2010). The "Recessive Strategy" (*e1e2e3*): in the triple-recessive background, the flavonoid share jumps to ~10%. This indicates a high degree of metabolic specialization (Lee et al., 2011). Despite having a lower total phenolic "budget," these plants allocate a significantly larger portion of it specifically to flavonoids (Zhu et al., 2018).

The genotype *e1E2e3* deserves special attention. It displays a "hybrid" metabolic signature: a TPC similar to other ND lines but a remarkably stable flavonoid ratio. While the 9-hour ShD treatment typically boosts absolute flavonoid levels, the relative share in *e1E2e3* remained fixed at 5.11% in both experimental groups.

This stability points toward the *E2* locus (the *GIGANTEA* ortholog) as a metabolic stabilizer. *GIGANTEA* is known to link the circadian clock with various physiological processes (Lin et al., 2021, Jiang et al., 2014); in this context, it may act as a homeostatic regulator that prevents the over-allocation of resources to the flavonoid pathway, ensuring a balanced phenolic profile regardless of the early-season photoperiodic "noise" (Josipović et al., 2016).

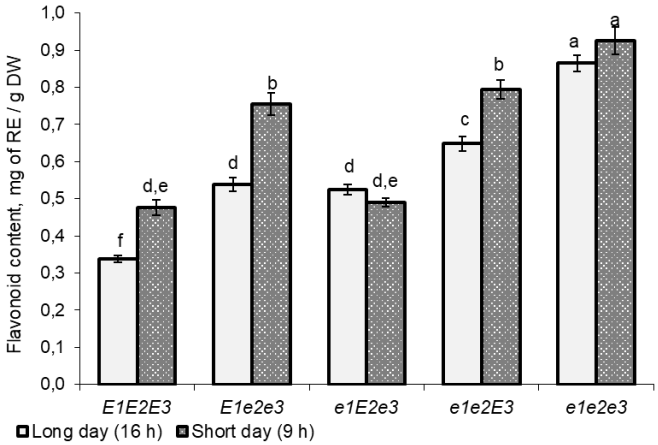

Fig. 2. Flavonoid content in seeds of soybean isolines differing in *E* gene alleles under different photoperiodic treatments, mg of RE / g DW (Long day – 16 h, Short day – 9 h; n = 10, x ± SD). Comparisons were made between different isolines and photoperiodic conditions. Different letters indicate statistically significant differences based on Tukey's post hoc test ($p < 0.05$).

Table. Partitioning of flavonoids within the total phenolic pool (Flavonoid-to-Total Phenolic ratio) in seeds of soybean isolines differing in *E* gene alleles under different photoperiodic treatments (n = 10, x ± SD)

Isoline genotype	Photoperiodic reaction	Flavonoid/Total Phenolic Ratio (%)	
		Long day – 16 h	Short day – 9 h
E1E2E3	short-day (ShD) line	2.34 ± 0.07^{e}	2.63 ± 0.12^{e}
E1e2e3	short-day (ShD) line	4.48 ± 0.16^{d}	$4.87 \pm 0.19^{c,d}$
e1E2e3	neutral-day (ND) lines	5.11 ± 0.13^{c}	5.11 ± 0.13^{c}
e1e2E3	neutral-day (ND) lines	5.11 ± 0.15^{c}	6.19 ± 0.20^{b}
e1e2e3	neutral-day (ND) lines	10.17 ± 0.25^{a}	9.93 ± 0.40^{a}

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

The fact that a 14-day ShD treatment at the V3 stage impacts the seed composition weeks later points to a "metabolic memory" effect. In ShD-sensitive lines (*E1*-carrying), the 9-hour induction likely accelerates the reproductive program (Yuhno and Zhmurko, 2010), which in turn upregulates the entire phenylpropanoid machinery. However, in ND lines, the response is more targeted. The 9-hour pulse acts as a signal to specifically enhance flavonoid synthesis without significantly altering the total phenolic baseline.

In conclusion, the genetic transition from photoperiodic sensitivity to neutrality is not a simple "loss-of-function" event. Instead, it represents a reprogramming of the seed metabolome. By reducing the dominance of the *E* loci, soybean plants switch from a generalized phenolic accumulation strategy to a specialized flavonoid-rich profile. For breeders, this means that selecting for early-maturing, photoperiod-insensitive varieties may inherently result in seeds with higher concentrations of bioactive flavonoids, enhancing the functional and nutritional quality of the crop (Ali et al., 2020, Lee et al., 2011).

Conclusions

The present study provides compelling evidence that the genetic system of soybean maturity genes (*E1, E2,* and *E3*) acts as a sophisticated metabolic regulator, orchestrating the partitioning of secondary metabolites in seeds. Our findings through the analysis of isogenic lines reveal several key conclusions:

1. The maturity genes do not only dictate the timing of flowering and maturation but also function as "metabolic switches" for the phenylpropanoid pathway. Dominant alleles, particularly *E1*, promote a high-output strategy for total phenolic compounds, whereas recessive alleles favor a shift toward specialized flavonoid biosynthesis.

2. We identified a possible metabolic trade-off between total phenolic quantity and flavonoid specificity. Photoperiod-neutral lines (*e1e2e3*) exhibit a significantly higher flavonoid-to-phenolic ratio (reaching up to 10%), which is four times higher than that of short-day sensitive genotypes. This suggests that breeding for early maturity and photoperiodic insensitivity inherently selects for a more specialized flavonoid-rich seed profile.

3. Short-day photoperiodic induction (9-hour) at the vegetative stage (V3-V5) is sufficient to reprogram the seed metabolome. This "metabolic memory" confirms that early-season environmental signals trigger long-term epigenetic or transcriptional shifts that persist until seed desiccation.

4. While *E1* is the primary driver of total phenolic accumulation, *E2* functions as a biochemical stabilizer. Its presence in certain genetic backgrounds (*e1E2e3*) provides metabolic buffering, maintaining a consistent flavonoid proportion regardless of fluctuations in day length.

These results have significant implications for "precision breeding". To develop soybean varieties with high antioxidant and functional value (high flavonoid content), breeders should focus on combinations of recessive e alleles. Conversely, for varieties where structural robustness or high total phenolic content is required, dominant *E* genotypes are preferable.

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ВПЛИВ АЛЕЛЬНОЇ ВАРІАТИВНОСТІ ГЕНІВ *E* НА ЗАГАЛЬНИЙ ВМІСТ ФЕНОЛЬНИХ СПОЛУК І НАКОПИЧЕННЯ ФЛАВОНОЇДІВ У НАСІННІ СОЇ (*GLYCINE MAX* (L.) MERR.)

Мета. Дослідити вплив ранньої фотоперіодичної індукції (стадія V3–V5) на розподіл фенольних сполук і флавоноїдів у насінні майже ізогенних ліній (МІЛ) сої з різними комбінаціями генів скороспілості (*E1–E3*). ***Методи.*** Об'єктами були майже ізогенні лінії сої (*Glycine max* (L.) Merr.): короткоденні (ShD: *E1E2E3, E1e2e3*) та нейтральноденні (ND: *e1E2e3, e1e2E3, e1e2e3*). Рослини піддавали впливу природного дня (16 год) або індуктивного короткого дня (9 год) протягом 14 днів із подальшим вирощуванням до дозрівання. Визначали загальний вміст фенолів (ЗВФ) та флавоноїдів. ***Результати.*** Виявлено ефект «метаболічної пам'яті»: рання індукція визначає кінцевий метаболом насіння. ShD лінії (з *E1*) мали значно вищий ЗВФ, особливо за 9-годинної індукції. ND-лінії продемонстрували нижчий ЗВФ, але суттєвий зсув у бік флавоноїдів. Рецесивний генотип *e1e2e3* мав найвищий вміст флавоноїдів і чотирикратне зростання їхньої частки відносно ЗВФ у порівнянні з ShD лінією *E1E2E3*. Генотип *e1E2e3* виявився метаболічно стабільним незалежно від режиму освітлення. ***Висновки***. Гени *E*-серії діють як «метаболічні воротарі»: домінантні алелі стимулюють загальне накопичення фенолів, тоді як рецесивні – активують спеціалізований синтез флавоноїдів. Генетична нейтральність до фотоперіоду сприяє збагаченню флавоноїдного профілю насіння.

Ключові слова: насіння сої (*Glycine max* (L.) Merr.), ізогенні лінії, гени *E*, фотоперіод, флавоноїди, фенольні сполуки.

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