Journal of Food Science and Technology (Iran)

Homepage:www.fsct.modares.ir

Scientific Research

# Gene Expression Profiling of Glycoalkaloid Biosynthesis in Potato Tubers in Response to Post-Harvest Storage Stress

Enas Ibrahim Khalil, Rafea Zaidan Mukhlif Al_Sugmany

Department of Biology, College of Sciences, University of Tikrit

**ARTICLE INFO**

**Article History:**

Received: 2025/11/20
Accepted: 2026/01/06

**Keywords:**

Potato,

Solanine,

*Solanum tuberosum*,

glycoalkaloids,

post-harvest pathology,

food safety,

biosynthetic genes.

DOI: 10.48311/fsct.2026.117818.82945

*Corresponding Author E-Mail:
enas.ibrahim@st.tu.edu.iq,

enas.ibrahim99kh@gmail.com

**ABSTRACT**

This study investigated the impact of post-harvest storage conditions on the biosynthesis of the toxic steroidal glycoalkaloids (SGAs), α-solanine and α-chaconine, in three potato cultivars (Arizona, Burren, and Lady Rosetta). Tubers were stored for 20 days under three regimes: optimal refrigeration (4°C), continuous light, and complete darkness. A combined molecular and chemical analysis was subsequently performed. Gene expression levels of key SGA biosynthetic genes (Hmg1, Pss1, Sgt1, Sgt2, Sgt3) were quantified using RT-qPCR, while SGA accumulation was measured via HPLC. The results demonstrated that storage environment profoundly influenced both transcriptional activity and metabolite levels. Refrigeration at 4°C effectively suppressed the expression of all five biosynthetic genes, resulting in negligible SGA concentrations across all cultivars. In stark contrast, light exposure acted as a powerful inducer, triggering significant gene upregulation and a substantial accumulation of SGAs, with α-solanine concentrations increasing over tenfold. Interestingly, dark storage also induced gene expression and SGA accumulation to levels markedly higher than refrigeration, though generally lower than light storage, identifying darkness as a sub-optimal stressor. This study conclusively demonstrates that improper storage induces glycoalkaloid biosynthesis at the transcriptional level. It confirms refrigeration as the only tested method that mitigates this health risk by maintaining low biosynthetic gene expression, thereby preserving tuber chemical safety and underscoring the critical importance of post-harvest management in the potato supply chain.

## 1-INTRODUCTION

The potato (*Solanum tuberosum* L.) is a cornerstone of global food security, yet its inherent production of steroidal glycoalkaloids (SGAs), primarily α-solanine and α-chaconine, presents a significant toxicological challenge [1]. While these compounds serve as a natural defense mechanism for the plant in the field, their accumulation post-harvest poses a direct risk to consumer health, with potential effects ranging from gastrointestinal distress to neurological disorders. The established triggers for SGA biosynthesis are physical damage and light exposure, leading to greening [2]. However, a critical and less quantified stressor exists within the post-harvest supply chain: sub-optimal ambient storage (warm, humid, dark) [3].

Dark, characterized by elevated humidity, temperature fluctuations, and the presence of wound and rot pathogens (*Fusarium*, *Erwinia*, etc.), represents a complex biotic and abiotic stress. It is well-documented that such conditions correlate with increased SGA concentrations [4]. However, the existing body of literature primarily relies on analytical chemistry methods (e.g., HPLC, LC-MS) to quantify the final toxic metabolites. This is a reactive approach; by the time elevated SGAs are detected, the tubers are often already unmarketable, leading to economic waste and potential safety breaches [5].

A proactive, mechanistic understanding of SGA induction is paramount for the food industry to develop predictive models and superior storage protocols. The biosynthetic pathway of solanine and chaconnes is well-elucidated, with key genes such as *SQS* (squalene synthase), *SSR2* (sterol side chain reductase 2), and *SGT1* (sterol glycoalkaloid glycosyltransferase 1) acting as critical control points [6]. The central hypothesis of this work is that dark conditions act as a potent inducer of the transcriptional activity of these key SGA biosynthetic genes. Understanding the expression of genes involved in steroidal glycoalkaloid (SGA) biosynthesis is a key step in potato breeding programs aimed at reducing the accumulation of these toxic compounds. Unlike traditional methods such as chemical analysis or marker-assisted selection (MAS), tracking biosynthetic gene expression is easier and more efficient [7]. SGAs are produced through the steroidogenic branch of the melonic acid/isoprenoid pathway, which includes several key enzymes, such as Hmg1 and Pss1, responsible for the initial steps, as well as Sgt1, Sgt2, and Sgt3, which are involved in the addition of sugars to solanidine as shown in Figure 1 .Studies indicate that SGA accumulation is influenced by the genetic regulation of these enzymes in response to environmental factors [8]. Kritz et al. (2007) demonstrated a direct correlation between increased gene expression of Hmg1 and Pss1 and elevated SGA levels in potato, reflecting the importance of these genes in controlling the biosynthetic pathway of toxic compounds [9]. Therefore, this study moves beyond mere metabolite quantification to estimate the expression of toxin genes in potatoes subjected to defined ambient dark storage conditions (22°C, dark).

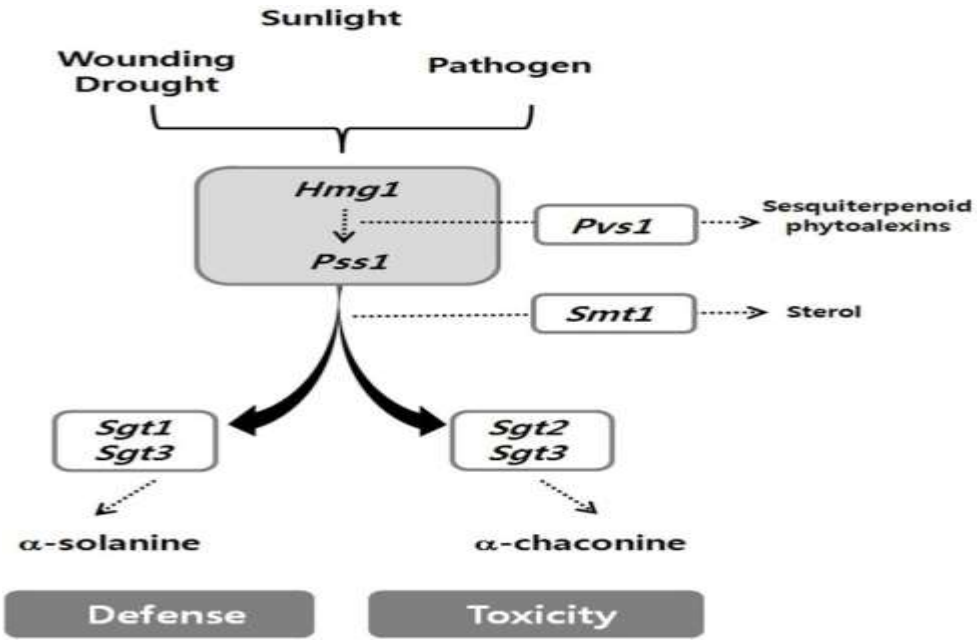


**Fig. 1.** Steroidal glycoalkaloid biosynthetic pathway in potato plants (8)

## 2-MATERIALS AND METHODS

### 2.1. Plant Material and Experimental Design

Tubers of three potato (*Solanum tuberosum* L.) cultivars—Lady Rosetta, Arizona, and Burren—were sourced directly from local farmers immediately after harvest. Dirt and impurities were removed. Tubers were subjected to a 20-day post-harvest storage trial under three distinct conditions:

1. Optimal Control Storage: Tubers were stored in darkness at 4°C in a controlled refrigeration unit.

2. Light Stress Storage: Tubers were exposed to continuous fluorescent light (intensity: ~50 µmol $m^{-2}$ $s^{-1}$) at ambient temperature (22 ± 2°C).

3. Dark Stress Storage: Tubers were stored in complete darkness at ambient temperature (22 ± 2°C).

For each cultivar and storage condition, three biological replicates were prepared, each consisting of a pooled sample from five individual tubers.

### 2.2. Extraction and Quantification of Glycoalkaloids by HPLC

The concentrations of the major steroidal glycoalkaloids (SGAs), α-solanine and α-chaconine, were quantified via high-performance liquid chromatography (HPLC) according to the method of Friedman et al. (2003) [10] with modifications.

Briefly, one gram of freeze-dried tuber powder was homogenized in 20 mL of 5% (v/v) aqueous acetic acid and shaken for 2 hours at room temperature. The homogenate was filtered through No. 42 filter paper (Whatman, UK). The filtrate was basified to pH ~10 with ammonium hydroxide ($NH_4OH$) and heated at 70°C for 50 minutes to hydrolyze esters. After cooling, the extract was incubated at 4°C for 24 hours to precipitate SGAs. The precipitate was recovered by centrifugation at 13,000 × *g* for 10 minutes at 4°C, redissolved in methanol, and re-centrifuged. The final supernatant was filtered through a 0.45 µm polyvinylidene difluoride (PVDF) syringe

filter (Pall Corporation, USA) prior to injection.

Chromatographic separation was performed on an Alliance 2695 HPLC system (Waters Corporation, USA) equipped with an Inertsil NH2 column (5 µm, 4.0 × 250 mm; GL Sciences, Japan) and a 2996 photodiode array detector (Waters). The mobile phase consisted of acetonitrile and 20 mM potassium phosphate buffer ($KH_2PO_4$, pH 7.0) (80:20, v/v), delivered isocratically at a flow rate of 0.7 mL/min. SGAs were detected at 208 nm. Identification was based on retention time and UV spectrum comparison with authentic standards: α-solanine (Sigma-Aldrich, USA) and α-chaconine (Extrasynthese, France). Quantification was achieved using a five-point external calibration curve ranging from 3.1 to 25.0 mg/L for each standard. Results are expressed as mg of SGA per 100 g of dry tuber weight.

### 2.3. Gene Expression Analysis by Quantitative Real-Time PCR (RT-qPCR)

#### 2.3.1. RNA Extraction and cDNA Synthesis

Total RNA was extracted from approximately 100 mg of frozen tuber cortex tissue (pooled from three tubers per replicate) ground in liquid nitrogen. TransZol Up Plus RNA Kit (TransGen Biotech, China) was used according to the manufacturer's protocol. RNA concentration and purity were assessed spectrophotometrically (A260/A280 and A260/A230 ratios), and integrity was verified via 1.5% agarose gel electrophoresis. RNA was stored at -80°C.

First-strand complementary DNA (cDNA) was synthesized from 1 µg of total RNA using the PrimeScript RT Master Mix (abm, Canada) in a 20 µL reaction, following the manufacturer's instructions. The thermal profile consisted of 42°C for 15 minutes and 85°C for 5 seconds in a Mastercycler thermocycler (Eppendorf, Germany).

#### 2.3.2. Quantitative Real-Time PCR (qPCR)

Gene-specific primers for key SGA biosynthetic genes and the reference gene (*GAPDH*) were designed using Primer-BLAST (NCBI) to ensure specificity (Table 1). qPCR reactions were performed in 20 µL volumes containing 10 µL of 2× SYBR Green Master Mix (Tinzyme, China), 0.5 µL of each primer (10 µM), 2 µL of diluted cDNA (1:10), and 7 µL of nuclease-free water. Reactions were run in triplicate on a Rotor-Gene Q thermocycler (Qiagen, Germany) with the following program: initial denaturation at 95°C for 2 min; 40 cycles of 95°C for 6 sec, 60°C for 30 sec, and 72°C for 20 sec. A melt curve analysis (65–95°C, increment 0.5°C) was performed post-amplification to confirm primer specificity and absence of primer-dimer artifacts.

#### 2.3.3. Data Analysis

Cycle threshold (Ct) values were determined automatically by the instrument software. Relative gene expression was calculated using the $2^{-\Delta\Delta Ct}$ method [11], with *GAPDH* as the endogenous control and tubers from the optimal control storage (4°C, dark) as the calibrator sample for each respective cultivar. Results are presented as mean fold-change in gene expression (± standard error) relative to the control.

**Table 1.** Primer sequence of one housekeeping gene and SGA-biosynthetic genes used for qRT-PCR analysis.

| Name | Type | Sequence | Bp | No. of bases |
|---|---|---|---|---|
| **Hmg1** | F | GGGTACAGTGGGTGGTGGAAC | 143 | 21 |
| | R | CACCAGCAAGAACAGAACC | | 19 |
| **Pss1** | F | CTTGCAGAGACTCGGGAACCTTG | 133 | 23 |
| | R | CGGTTGCCAGAAAGTTGTGC | | 20 |
| **Sgt1** | F | GGTTTACAGACCTCACAAGCAGCC | 191 | 24 |
| | R | CAATGCCATAGCTTCGTTCCTCCG | | 24 |
| **Sgt2** | F | GCAGTCGGAGGATTCATGACACAC | 190 | 24 |
| | R | TCGATATCTCAGCACCTCCGTTGG | | 24 |
| **Sgt3** | F | GTTTATCATCCAAGGCTGGGCACC | 192 | 24 |
| | R | GTTTATCATCCAAGGCTGGGCACC | | 24 |
| **GADPH** | F | CTCCGCTCCTAGCAAAGATG | 168 | 20 |
| | R | GTGGTCATGAGACCCTCCAC | | 20 |

## 3-RESULTS

### HPLC analysis

The concentrations of α-solanine and α-chaconine were determined of the active compounds Alpha-solanine and Alpha-chaconine in three potato cultivars (Arizona, Burren, Lady Rosetta) under three different conditions: (storage at a cold temperature of 4°C (refrigerator), and storage to both light and darkness) for 20 days, using high-performance liquid chromatography (HPLC) technique as show in Table 2. In refrigerated samples, the results showed that Arizona and Burren had the same concentration of alpha-solanine (0.04 mg/100g), while a significantly lower concentration was observed in Lady Rosetta (0.1 mg/100g). Alpha-chaconine was similar in Arizona and Burren (0.024), and relatively lower in Lady Rosetta (0.018). These results demonstrate that Lady Rosetta naturally contains lower levels of alkaloids than other cultivars.

Exposure of samples to light significantly increased alpha-solanine concentrations in all types of potato, reaching 3.3 in Arizona and 3.1 in Burren, while the highest value was recorded in Lady Rosetta (3.9). Alpha-chaconine concentration also increased to 0.04 in Arizona and 0.03 in both Burren and Lady Rosetta. This increase suggests that light stimulates metabolic activity associated with alkaloid production, as part of the photoprotective mechanism in potato.

When samples were exposed to darkness, alpha-solanine concentrations remained relatively high compared to the control samples, but were lower than under light, reaching 3.0 in Arizona, 1.8 in Burren, and 3.8 in Lady Rosetta. Alpha-chaconine, however, reached 0.03 in Arizona and 0.02 in both Burren and Lady Rosetta. This suggests that darkness does not stimulate alkaloid production to the same extent as light, but

does not completely prevent their accumulation.

Table 2- Concentrations of active ingredients in the studied potato samples

| Sample | α-solanine mg per 100 g dry weight | α-chaconine mg per 100 g dry weight |
|---|---|---|
| Refrigerator at 4°C | | |
| Arizona - | 0.4 | 0.024 |
| Burren - | 0.4 | 0.024 |
| Lady Rosetta - | 0.1 | 0.018 |
| Light at 22°C | | |
| Arizona - | 3.3 | 0.04 |
| Burren - | 3.1 | 0.03 |
| Lady Rosetta - | 3.9 | 0.03 |
| Dark at 22°C | | |
| Arizona - | 3.0 | 0.03 |
| Burren - | 1.8 | 0.02 |
| Lady Rosetta - | 3.8 | 0.02 |

**Expression pattern of SGA -biosynthetic genes in tubers of Burren, Arizona, and Lady Rosetta under sunlight compared with dark storage**

The expression pattern of SGA-biosynthetic genes was determined in the tuber of Burren, Arizona, and Lady Rosetta plants exposed after 20 days of storage in different conditions. In the present study, a significant difference was observed in the transcript levels of five key genes in the tubers of Burren, Arizona, and Lady Rosetta exposed to proper storage at a cold temperature of 4°C and poor storage to both light and darkness for 20 days. The transcript levels of Hmg1, Pss1, Sgt1, Sgt2, and Sgt3 were significantly higher in tubers stored under stress conditions (light or darkness) compared to those stored optimally at 4°C. Tubers stored under light exhibited the highest fold-change in gene expression. These results indicate that light exposure is a clear inducer of SGA-biosynthetic gene expression. For instance, in the Lady Rosetta cultivar, the transcript level of *Sgt3* reached an impressive 68.5 under sunlight, significantly higher than in dark conditions (30.0). This suggests that light may activate certain metabolic pathways or transcription factors that enhance SGA synthesis, the expression of these genes being repressed in the three cultivars (Table 3).

Table 3. The relative transcript levels of SGA biosynthetic genes in potato tubers of burren, Arizona, and Lady Rosetta under different condition storage (refrigerator at 4°C, Sun light and dark) relative to the optimal refrigeration control (4°C, dark).

Transcript level of SGA-biosynthetic genes

| Potato Cultivar | Storage conditions | *Hmg1* | *Pss1* | *Sgt1* | *Sgt2* | *Sgt3* |
|---|---|---|---|---|---|---|
| Burren | refrigerator at a 4°C | 0.5 | 0.50 | 0.49 | 0.48 | 0.49 |
| | Sun light | 2.92 | 1.88 | 2 | 1.99 | 45.65 |
| | Dark | 1.15 | 1.6 | 1.64 | 0.71 | 20.41 |
| Arizona | refrigerator at a 4°C | 0.06 | 0.13 | 0.13 | 0.06 | 0.12 |
| | Sun light | 2.34 | 3.73 | 2.48 | 1.61 | 4.63 |
| | Dark | 0.23 | 0.51 | 0.31 | 0.25 | 3.41 |
| Lady Rosetta | refrigerator at a 4°C | 0.50 | 0.02 | 0.48 | 0.21 | 0.02 |
| | Sun light | 7.35 | 2.38 | 1.39 | 0.84 | 68.5 |
| | Dark | 4.80 | 0.11 | 1.19 | 0.43 | 30.0 |

3-hydroxy-3-methylglutaryl coenzyme A reductase 1 (*Hmg1*), squalene synthase 1 (*Pss1*), solanidine galactosyl transferase (*Sgt1*), solanidine glucosyl transferase (*Sgt2*) and rhamnosyl transferase (*Sgt3*).

## 4- Discussion

Steroidal alkaloids, such as α-solanine and α-chaconine, are natural defense compounds produced by plants, including potatoes, as a defense against pathogens and stressful environmental conditions [12,13]. In present study, the results show Lady Rosetta contains the lowest number of alkaloids at low temperatures (4°C). This is due to slower biological processes within the tuber cells, including enzyme activity associated with alkaloid synthesis. Alkaloids are compounds produced by tubers in response to stress, such as wounds, light, or high temperatures. Therefore, in cold conditions, the metabolic activity associated with the production of these compounds decreases [14-16].

The results indicate that light is one of the most powerful environmental stimuli affecting the metabolic pathways responsible for the synthesis of these alkaloids. All three cultivars (Arizona, Burren, and Lady Rosetta) showed significantly increased concentrations of α-solanine and α-chaconine after light exposure. This is consistent with previous studies, such as Friedman's (2006) study, which demonstrated that light stimulates the conversion of sugars to alkaloids by activating the expression of

enzymes responsible for the alkaloid biosynthesis pathway [13].

This stimulation is linked to a biological defense mechanism wherein alkaloids act as antifungal and antibacterial agents, and also serve as a response to photo-oxidative damage. Exposure to light also stimulates chlorophyll production, which often coincides with an increase in alkaloids and explains the green color of potato tubers when exposed to light [17,18].

Under dark conditions, α-solanine and α-chaconine concentrations were higher than in the control group but lower than in the light, suggesting that alkaloid accumulation does not absolutely require light but may occur to a lesser extent as a result of ongoing basal metabolic activity within the tuber, especially at relatively high temperatures or during prolonged storage. According to Urban et al. (2018), non-light factors such as humidity, heat, and mechanical injury can also contribute to stimulating alkaloid production, albeit to a lesser extent than light [18]. On the other hand, it is noted that the Lady Rosetta variety showed the highest accumulation of alkaloids under light, despite having the lowest concentrations in its natural state. This indicates that it is more responsive to environmental stimuli, which may be related to its genetic characteristics and the genetic makeup that controls the expression of enzymes that catalyze alkaloid biosynthesis [19].

Expression analysis of SGA-biosynthetic genes could be applied as a selection tool for potato cultivars with low SGA content. Postharvest potatoes are prone to greening when exposed to light during storage, transportation, or sales. Hossain et al. (2015) reported that SGA accumulation was induced by factors such as temperature, light, and storage duration. Thus, we used three different storage conditions treatment in Burren, Arizona, and Lady Rosetta, for the selection of genes which could be applied for screening potato cultivars with high SGA content. qRT-PCR analysis of the storage-stressed potatoes successfully uncovered mRNAs involved in SGA accumulation. Two genes, *Hmg1* and *Pss*, involved directly in the SGA biosynthesis pathway, catalyse the first step in SGA biosynthesis that increases in response to external stress, including wounding, plant disease, and development. Hence, the use of expression levels of *Hmg1* and *Pss1* under storage stress increases the efficiency of selecting potato clones with low SGA content, which can be cultivated in various environmental conditions. The results demonstrate that light exposure significantly enhances the accumulation of alpha-solanine in potato cultivars, suggesting an environmental influence on glycoalkaloid biosynthesis. While alpha-chaconine levels showed less variability, their presence alongside elevated alpha-solanine highlights the importance of monitoring both compounds for assessing the safety and quality of potato cultivars. Sunlight storage resulted in the higher expression of genes encoding SGA biosynthetic enzymes in tubers of Burren compared to those in tubers of Arizona and Lady Rosetta, indicating that light treatment made a significant difference in the gene expressions between Burren and both Arizona and Leady (Table 2). In addition, an increase in the transcript abundance of *Sgt1*, *Sgt2,* and *Sgt3* at sunlight exposure indicated their direct involvement in glycoalkaloid accumulation. Increased transcript levels of *Hmg1* and *Pss1* in the upstream of the pathway under light stress showed that they might play a role in the regulation of *Sgt1*, *Sgt2,* and *Sgt3* levels in the downstream of the pathway. The expression levels of *Sgt1* and *Sgt2* were relatively associated with the content of the solanine-to-chaconine ratio, respectively.

## 5- Conclusion

This study provides unequivocal molecular evidence that ambient dark storage serves as a potent transcriptional activator of the glycoalkaloid biosynthetic pathway in potato tubers. Our gene expression analysis demonstrates a significant and rapid upregulation of key genes, including *Hmg1* ، *Pss1* ،*Sgt1/2/3*, in response to the combined biotic and abiotic stresses of pathogen presence and improper humidity. This upregulation precedes the substantial accumulation of α-solanine and α-chaconine to levels detectable by conventional chemical analysis, highlighting a critical "lag-time" where the toxin threat is developing but not yet measurable in the final product. The implications for the food industry are substantial. First, these findings underscore that sanitation is not merely a matter of controlling rot and spoilage but is a direct and critical control point for chemical food safety. Second, we have identified specific genetic biomarkers whose expression can serve as an early-warning system. The transition from post-hoc chemical analysis to predictive molecular diagnostics represents a paradigm shift in quality assurance for the potato supply chain. Future work should focus on translating this knowledge into practical industrial tools. This includes the development of rapid, cost-effective biosensors or PCR-based kits capable of assessing the "toxin gene expression status" of stored potatoes. Furthermore, these genetic markers can be used to benchmark and optimize storage technologies and sanification protocols, ensuring they effectively suppress the molecular initiation of toxin production. By integrating this molecular understanding into supply chain management, the industry can proactively mitigate glycoalkaloid risk, enhancing both consumer safety and reducing economic losses, thereby fortifying the integrity of one of the world's most vital food commodities.

## 6- REFERENCES


[1] Friedman, M. (2006). Potato glycoalkaloids and metabolites: roles in the plant and in the diet. *Journal of agricultural and food chemistry*, *54*(23), 8655-8681.

[2] Milner, S. E., Brunton, N. P., Jones, P. W., O'Brien, N. M., Collins, S. G., & Maguire, A. R. (2011). Bioactivities of glycoalkaloids and their aglycones from Solanum species. *Journal of agricultural and food chemistry*, *59*(8), 3454-3484.

[3] Okoth, M. (2016). A review of occurrence of glycoalkaloids in potato and potato products. *Current Research in Nutrition and Food Science Journal*.

[4] Petersson, E. V., Arif, U., Schulzova, V., Krtkova, V., Hajslova, J., Meijer, J., ... & Sitbon, F. (2013). Glycoalkaloid and calystegine levels in table potato cultivars subjected to wounding, light, and heat treatments. *Journal of Agricultural and Food Chemistry*, *61*(24), 5893-5902.

[5] Ginzberg, I., Tokuhisa, J. G., & Veilleux, R. E. (2009). Potato steroidal glycoalkaloids: biosynthesis and genetic manipulation. *Potato Research*, *52*(1), 1-15.

[6] Itkin, M., Heinig, U., Tzfadia, O., Bhide, A. J., Shinde, B., Cardenas, P. D., ... & Aharoni, A. (2013). Biosynthesis of antinutritional alkaloids in solanaceous crops is mediated by clustered genes. *Science*, *341*(6142), 175-179.

[7] Cárdenas, P. D., Sonawane, P. D., Heinig, U., Bocobza, S. E., Burdman, S., & Aharoni, A. (2015). The bitter side of the nightshades: Genomics drives discovery in Solanaceae steroidal alkaloid metabolism. *Phytochemistry*, *113*, 24-32.

[8] Sawai, S., Ohyama, K., Yasumoto, S., Seki, H., Sakuma, T., Yamamoto, T., ... & Umemoto, N. (2014). Sterol side chain reductase 2 is a key enzyme in the biosynthesis of cholesterol, the common precursor of toxic steroidal glycoalkaloids in potato. *The Plant Cell*, *26*(9), 3763-3774.

[9] Krits, P., Fogelman, E., & Ginzberg, I. (2007). Potato steroidal glycoalkaloid levels and the expression of key isoprenoid metabolic genes. *Planta*, *227*(1), 143-150.

[10] Friedman, M., Roitman, J. N., & Kozukue, N. (2003). Glycoalkaloid and calystegine contents of eight potato cultivars. *Journal of agricultural and food chemistry*, *51*(10), 2964-2973.

[11] Livak, K. J., & Schmittgen, T. D. (2001). Analysis of relative gene expression data using real-time quantitative PCR and the 2−ΔΔCT method. *methods*, *25*(4), 402-408.

[12] Sharma, R. K., Coniglio, M. A., & Laganà, P. (2021). The role of glycoalkaloids, lipids, and proteins in tissue inflammation. In *Natural Inflammatory Molecules in Fruits and Vegetables* (pp. 27-37). Cham: Springer International Publishing.

[13] Friedman, M. (2006). Potato glycoalkaloids and metabolites: roles in the plant and in the diet. *Journal of agricultural and food chemistry*, *54*(23), 8655-8681.

[14] Li, R., Wang, B., Chen, W., Zhang, C., Li, N., Wang, Y., ... & He, J. (2025). Effect of potato glycoside alkaloids on mitochondria energy metabolism of Fusarium solani, the root rot pathogen of Lycium barbarum. *Frontiers in Microbiology*, *15*, 1512027.

[15] Shanina, E. P., Oberiukhtin, D. A., & Chernitskiy, A. E. (2024). Potato juice vs. traditional potato use—a new insight. *Sel'skokhozyaistvennaya biologiya [Agricultural Biology]*, *59*(1), 22-38.

[16] Issa, A. Y., Volate, S. R., & Wargovich, M. J. (2006). The role of phytochemicals in inhibition of cancer and inflammation: New directions and perspectives. *Journal of Food Composition and Analysis*, *19*(5), 405-419.

[17] EFSA Panel on Contaminants in the Food Chain (CONTAM), Schrenk, D., Bignami, M., Bodin, L., Chipman, J. K., del Mazo, J., ... & Grasl-Kraupp, B. (2020). Risk assessment of glycoalkaloids in feed and food, in particular in potatoes and potato-derived products. *EFSA Journal*, *18*(8), e06222.

[18] Urban, J., Hamouz, K., Lachman, J., Pulkrábek, J., & Pazderů, K. (2018). Effect of genotype, flesh colour and environment on the glycoalkaloid content in potato tubers from integrated agriculture. *Plant, Soil & Environment*, *64*(4).

[19] Nitithamyong, A., Vonelbe, J. H., Wheeler, R. M., & Tibbitts, T. W. (1999). Glycoalkaloids in potato tubers grown under controlled environments. *American journal of potato research*, *76*(6), 337-343.

[20] Hossain, M. A., Bhattacharjee, S., Armin, S. M., Qian, P., Xin, W., Li, H. Y., ... & Tran, L. S. P. (2015). Hydrogen peroxide priming modulates abiotic oxidative stress tolerance: insights from ROS detoxification and scavenging. *Frontiers in plant science*, *6*, 420.