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A Review of the Health Impacts of Solanine: The Toxic Alkaloid Found in Potatoes

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ABSTRACT

Solanine, a steroidal glycoside found in potatoes, serves as a natural defense mechanism for the plant, exhibiting fungicidal and pesticidal properties that protect it from phytopathogenic fungi. This compound can be present in various parts of the plant, including the leaves, fruits, and tubers. However, control measures on solanum glycoside toxins are based on careful selection and seed potato varieties, and attention to handling and processing. In order to reduce the risks and ensure sustainable storage, potatoes should be stored in cool, dark areas. Solanine poisoning is primarily manifested by gastrointestinal and neurological disorders and may cause severe nervous and exanthematous syndrome. This review provides a comprehensive survey on glycoalkaloid distribution in potatoes and its associated factors, its impact on flavor, the neurotoxic effects of solanine on humans, the various analytical methods used for its evaluation, and strategies to control its formation.

1. Introduction

Solanum tuberosum L., commonly known as the potato, is the third major food crop in the world, after wheat and rice. From a nutritional, agricultural, and toxicological perspective, *Solanum tuberosum* has a special place, with its nutritional value and protein quality surpassing that of other cereals. It is considered the second most important crop in overall protein production after soybeans in the world (Sotelo & Serrano, 2000). According to the Food and Agriculture Organization of the United Nations, potato production reaches approximately 388 million tonnes annually (Loveniers, 2019). The demand for fresh potatoes is increasing in developing countries, where consumers prioritize the appearance of tubers, ensuring they are free from damage and diseases (Alamar et al., 2017). While Alkaloids in potato tubers are normally nontoxic, green or stressed potato tubers can contain levels of solanine that may be harmful (Hodgson, 2012). Glycoalkaloids, which are secondary metabolites found in potatoes, can be toxic to humans in high concentrations. The primary examples of this group, α-Solanine and α-chaconine, show anti-acetylcholinesterase activity (Roepcke, 2011). Potatoes displaying signs of greening, sprouting, or physical damage

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should not be consumed due to high content of solanine and chlorophyll, as the synthesis of chlorophyll leads to an increase in solanine concentration in the potato peels. This biochemical process is induced by light exposure (Omayio et al., 2016).

The amount of solanine is high in the green layer of the potato, and there may be increased content in other parts of the potato. A number of factors, such as injury, fungal attack, inappropriate growing conditions, climate, and most importantly, insufficient storage conditions, increase the glycoalkaloid concentration in the potato tuber (Sotelo & Serrano, 2000). Excessive exposure to light is the main factor in producing green potatoes. Solanine is produced as a deterrent to insects and diseases. On the other hand, it has been shown that α-solanine has some useful properties such as anti-cancer, anti-bacterial, and anti-diabetic (Chen et al., 2018).

It can cause oxidative stress-related impacts such as increased lipid peroxidation and reduced antioxidant markers (Gouhar et al., 2022). These reactions show unacceptable effects on shelf life, texture, and nutritional value of products and are one the causes of food deterioration (Sadighara et al., 2016).

According to published reports, cases such as acute poisoning, coma, and death due to the consumption of sprouted, stressed, and spoiled potatoes have been observed in humans, and these effects have been attributed to glycoalkaloids (Satarug, 2018). According to the World Health Organization (WHO) document, solanine normal and non-toxic level in potatoes is 20-100 mg per kg of potatoes (Kotsonis & Burdock, 2008).

1.1 Glycoalkaloid Distribution in Potatoes

Glycoalkaloids are present in most tissues of the potato plant, except for the pith, which represents the central part of the potato tuber. Table 1 lists the glycoalkaloid contents of different parts of the potato plant as discovered by several researchers. Glycoalkaloids are synthesized during the germination stage and reach their peak during the flowering period (Kipkoech, 2018). Specific tissues that have been found to contain glycoalkaloids include leaves, shoots, stems, blossoms, tubers, eyes, peels, and sprouts. Recent studies show that α-chaconine is the main glycoalkaloid that makes up the majority of potato sprouts (60%), while α-solanine is the second most dominant (40%). It is generally reported that the maximum glycoalkaloid concentration is associated with potato sprouts (Baur et al., 2021; Dusza et al., 2020).

Glycoalkaloids are not uniformly distributed in different plant tissues. Generally, the content of glycoalkaloid first increases in the leaves of the plant and then, with the new growth, its amount decreases significantly in the older leaves. Sprouts also contain the highest amounts of glycoalkaloids (Figure 1). Glycoalkaloids that are present in the roots and tubers are not transferred to the upper parts of the plant, and in general, there is little or no transport of glycoalkaloids between different parts of the plant. Therefore, considering that few people consume potato sprouts or leaves, the tuber itself is of major importance (Benkeblia, 2020). Recent studies show that most of the glycoalkaloids in normal potatoes are in the outer layers of the tuber, and if the potato is peeled, a relatively significant amount of glycoalkaloids is reduced. The amount of glycoalkaloid in potato peel compared to the rest of the tuber has been reported in the range of 30 to 80% (Dusza et al., 2020).

Table 1. The glycoalkaloid (GA) contents of different parts of the potato plant (mg/100 g)

Plant part	GA content	Reference
Leaves	230-1000	(Kozukue & Mizuno, 1990)
Stems	3071	
Tuber	-	
Peel	13-400	
Flesh	-	
Leaves	1450	(Friedman & McDonald, 1999)
Stems	320-450	
Tuber	-	
Peel	850	
Flesh	60100	
Leaves	-	(Sotelo & Serrano, 2000)
Stems	-	
Tuber	-	
Peel	7.17-91.63	
Flesh	0.63-8.37	
Leaves	-	(Friedman et al., 2003)
Stems	-	
Tuber	-	
Peel	84-2226	
Flesh	5-592	
Leaves	-	(Friedman, 2006)
Stems	-	
Tuber	-	
Peel (dehydrated powder)	83.8	
Flesh (dehydrated powder)	36.5	
Leaves	-	(Aziz et al., 2012)
Stems	-	
Tuber	-	
Peel	45.98-2742.6	
Flesh	4.01-2466.56	
Leaves	-	(Deußer et al., 2012)
Stems	-	
Tuber	-	
Peel	585-5342	
Flesh	7-466	
Leaves	-	(Ji et al., 2012)
Stems	-	
Tuber	0.605	
Peel	1.111	
Flesh	-	
Leaves	-	(Rytel et al., 2013)
Stems	-	
Tuber	5.48	
Peel	15.33	
Flesh		
Leaves	-	(Valcarcel et al., 2014)
Stems	-	
Tuber	-	
Peel	150-8133	
Flesh	4-957	
Leaves	-	(Romanucci et al., 2018)
Stems	-	
Tuber	8.74	
Peel	-	
Flesh	-	

1.2 Effect of glycoalkaloids on flavor

Potatoes exposed to sunlight during growth can develop a bitter taste, often accompanied by a scratchy sensation in the throat. This bitterness is primarily linked to high glycoalkaloid levels, though phenolic compounds may also contribute. Varieties with glycoalkaloid levels exceeding 14 mg/100 g are reported as bitter, and poor growing conditions can elevate these levels to 30 mg/100 g or more. Tests show that potatoes with over 140 mg/kg glycoalkaloids are bitter, while levels above 220 mg/kg can cause burning sensations in the mouth and throat (Friedman, 2006).

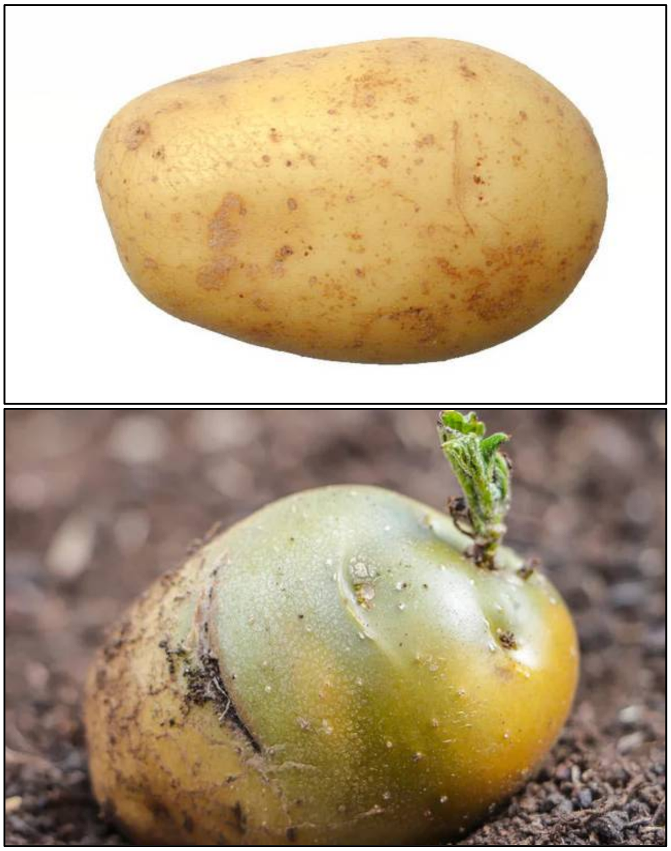

Figure 1. Comparison between a healthy potato (up) and a sprouted potato (down)

2. Discussion

2.1 Factors affecting glycoalkaloid content in potato

In this section, the effective factors of the formation of glycoalkaloids in potatoes will be investigated, and as a logical starting point, genetic differences inherent among potato varieties will be discussed first.

2.2 Climatic conditions

Studies from different countries show that the glycoalkaloid content of potato varieties can be very different. The glycoalkaloid content of different potato varieties in different countries is summarized in Table 2. Conflicting data have been reported relative to the influence of climate on the glycoalkaloid content of potatoes. Glycoalkaloid levels differ greatly in different potato varieties and may be affected by heat, light, precipitation, stress situations such as heat/cold and drought during plant growth and postharvest storage conditions, including mechanical injury and storage (Muñoa et al., 2022).

Table 2. Glycoalkaloid (GA) content (mg/100 g) of different potato varieties in different countries

Countries	GA content	Reference
Poland	8.22-18.09	(Rytel, 2012)
Denmark	852.4-868.4	(Nielsen et al., 2020)
Europe	2-156	(Rytel, 2012; Haase, 2010)
Kenya	3.5-17.5	(Kirui et al., 2009)
Pakistan	3-5449	(Aziz et al., 2012)
Canada	0.01-6.9	(Ji et al., 2012)
Italy	5.15-18.2	(Romanucci et al., 2018)
Mexico	0.63-8.37	(Sotelo & Serrano, 2000)
China	2.88-8.88	(Chen et al., 2018)
Poland	41.75-59.7	(Dusza et al., 2020)

2.3 Fertilization

Although nitrogen is an important chemical compound in potato production, an adequate supply of nitrogen can lead to the achievement of economically sustainable potato yields and also lead to the achievement of quality goals for potato production and processing. At the same time, it can affect the performance and quality of the tuber (Wen et al., 2019).

Najm et al. (2012) also found that the use of nitrogen fertilizer increased the glycoalkaloid concentration in potato tubers. However, Trejo-Escobar et al. (2019) found that the influence of fertilization on glycoalkaloid content varied depending on the potato. It has also been reported in a study that a high nitrogen fertilization rate decreased glycoalkaloid concentration in potato leaves (Fragoyiannis et al., 2001).

2.4 Storage Temperature and Time

Many studies in the context of storage temperature and time have shown that these factors can play an important role in the glycoalkaloid content in potato. According to the research conducted, it was shown that high temperature and reduced radiation increase the level of glycoalkaloids in potato leaves (Lafta & Lorenzen, 2000).

In addition, in some studies, different results have been stated regarding glycoalkaloid content in different parts of the potato during storage time. In such a way that the levels of glycoalkaloid in potato peel are different during storage, but they do not change in potato flesh (Nie et al., 2019).

Storage conditions and tuber type influence the levels of α-solanine and α-chaconine in potatoes. Glycoalkaloid levels tend to increase during storage, with green potatoes showing the most significant rise. Over time, these compounds distribute unevenly within potato tubers, with slight increases in the medulla, larger increases in the periderm, and the most substantial accumulation in sprouts (Deng et al., 2021).

On the other hand, based on a study conducted in 2020 in Poland, they concluded that during storage, the glycoalkaloid concentration in potatoes that were kept at 8°C for 5 months increased, and stress factors such as mechanical damage and Exposure to light can lead to a further increase in glycoalkaloid content in potato tubers (Dusza et al., 2020). On the other hand, in a report in 2010, it was shown that storing potatoes under cold conditions (cold storage) with low stress does not have a significant effect on the amount of glycoalkaloid compounds. This is while sprouting and pre-sprouting had a significant effect on the amount of glycoalkaloid. Haase (2010) also reported that controlled storage at high temperature (8°C) using sprout inhibitors was not effective, and this requires professional storage management.

2.5 Influence of light on glycoalkaloid content

Probably, light is the main factor of glycoalkaloid formation in potato. However, the effect of light on glycoalkaloid content in plants can be influenced by various factors. Idowu et al. (2022) in Nigeria found that the tubers of *Solanum tuberosum* and purple-fleshed potatoes exposed to sunlight had significantly increased glycoalkaloid content compared to non-exposed tubers, and consumption of these tubers may pose a threat to vital organs in rats. Furthermore, a study conducted in Brazil to determine the effect of two light sources and temperature on the total glycoalkaloid (TGA) content of cultivated potato tubers showed that exposure of potato tubers to fluorescent light resulted in the highest glycoalkaloid levels (Machado et al., 2007). Another study also showed that damaged tubers exposed to fluorescent light had higher levels of glycoalkaloids compared to undamaged tubers stored in the dark (Frydecka-Mazurczyk & Zgórska, 2001).

On the other hand, other findings showed that exposure of potato tubers to red light significantly increases the content of steroidal glycoalkaloids in this plant, while Yanlin et al. (2010) showed in his reports that violet light did not result in any accumulation. Mekapogu et al. (2016) also found that yellow light inhibited the expression of glycoalkaloid biosynthetic genes and led to lower levels of steroidal glycoalkaloid accumulation.

On the other hand, a study conducted by Shepherd et al. (2016) found that light exposure had little effect on α-solanine accumulation in transgenic potato tubers with reduced glycoalkaloid content. However, α-chaconin levels were significantly increased in the peel of both control and transgenic lines upon exposure to light. In addition, in the report of Okamoto et al. (2020) in the United Kingdom, it was shown that blue and red light wavelengths were effective in inducing and accumulating chlorophyll and glycoalkaloids in potato tubers, while darkness and far-red light prevented their accumulation.

2.6 Natural Resources of α-Solanine

Steroid alkaloids generally appear as glycosides, with their aglycones characterized by a C27-carbon skeleton derived from *cholestane*. These compounds can be categorized into five primary groups: *spirosolanes* (e.g., *solasodine*), *epiminocholestanes* (e.g., *solacongestidine*), *solanidanes* (e.g., *solanidine*), *solanocapsine* (e.g., *solanocapsine*), and *3-aminospirostanes* (e.g., *jurubidine*). Sapogenins represent the aglycone component of a family of natural products known as saponins (Manrique-Moreno et al., 2014).

Despite having nutritional compounds such as carbohydrates, vitamins (C or B_6), potatoes also contain other secondary compounds such as glycoalkaloids (Baur et al., 2021). Glycoalkaloid compounds (α-solanine and α-chaconine) are effective in creating the taste of potatoes, but in higher concentrations, they cause bitterness in potatoes, which can be toxic to humans. Solanine and chaconine have a similar chemical structure and differ only in the carbohydrate part. In this way, the carbohydrate part of solanine consists of galactose, glucose, and rhamnose units (β-solatriose), while in chaconine, there is glucose and two parts of rhamnose (β-chacotriose) (Figure 2) (Sotelo & Serrano, 2000). Their natural function is probably to serve as stress metabolites. Increases in solanine in the potato peel are closely associated with greening (synthesis of chlorophyll) of the peel. Koffi et al. (2017) highlighted that decayed potatoes, including green and sprouting ones, also contained high levels of toxic glycoalkaloids, including solanine.

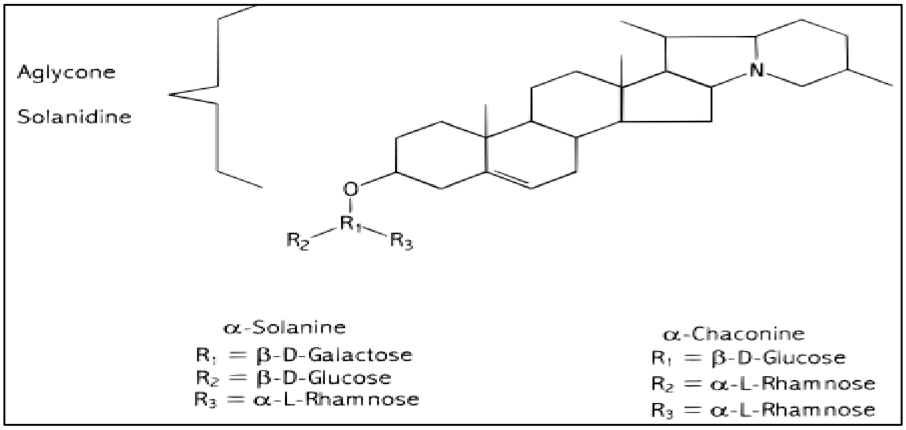

Figure 2. Structure of the solanidine alkaloids: R-solanine and R-chaconine (Sotelo & Serrano, 2000)

2.7 Steroidal Glycoalkaloid Biosynthesis and Intermediate Compounds in the Pathway

The biosynthesis of steroidal glycoalkaloids (SGAs) occurs in three major stages (Figure 3). The initial phase involves the formation of C5 isoprenoid units via the cytosolic mevalonate pathway, ultimately leading to the synthesis of farnesyl diphosphate (FPP). This key intermediate can either be converted into squalene and subsequently sterols or into sesquiterpenes such as rishitin. The second phase encompasses the conversion of 2,3-oxidosqualene into sterols, including cycloartenol and lanosterol, which are further metabolized into cholesterol, campesterol, and sitosterol-precursors of SGAs. The third stage, considered secondary metabolism, involves the transformation of cholesterol into solanidine, followed by glycosylation reactions yielding glycoalkaloids such as chaconine and solanine. This step is mediated by specific enzymes encoded by genes such as *SGT1*, *SGT2*, and *SGT3*. The biosynthetic pathway is tightly regulated by developmental cues and environmental stressors, and may operate independently from other terpene-derived pathways. Cytochrome P450 enzymes are implicated in several transformation steps. The structural diversity of SGAs across different potato species likely results from variation in both enzyme specificity and precursor availability (Ginzberg et al., 2009).

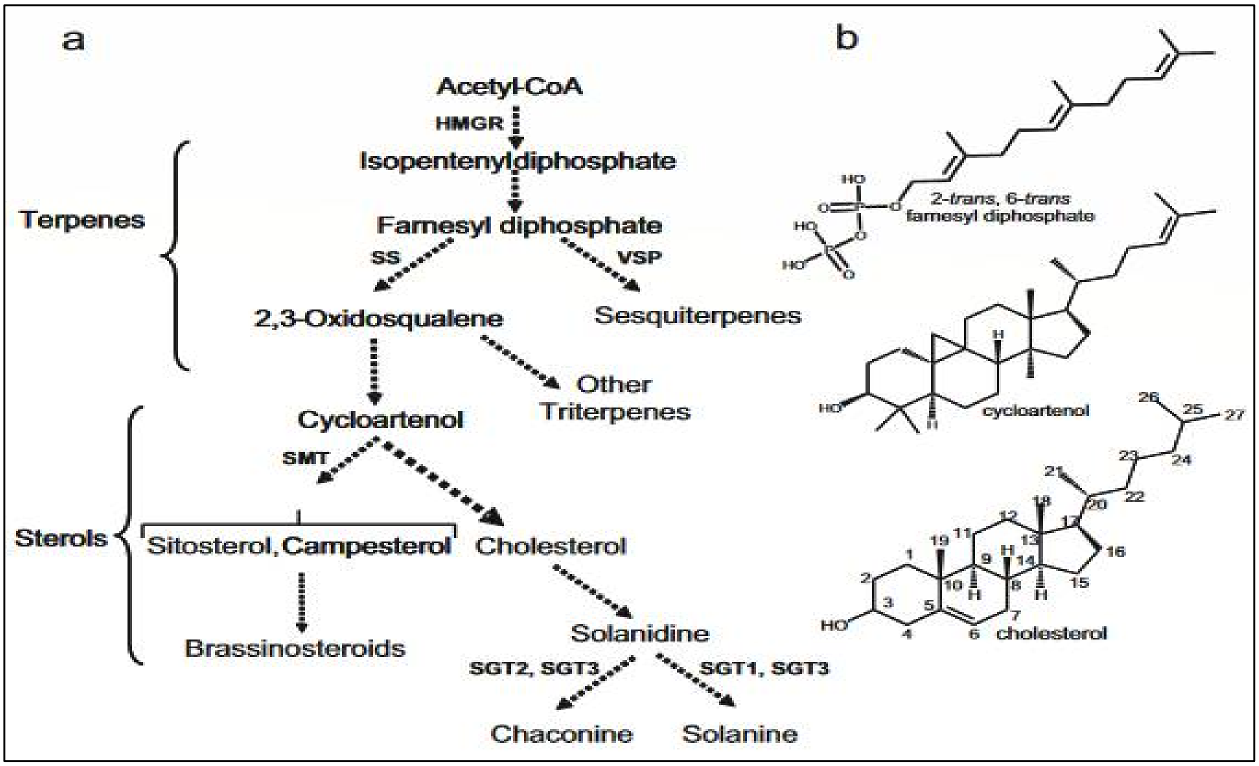

Figure 3. Illustrates a simplified biosynthetic pathway for steroidal glycoalkaloids

* Panel (a) depicts the biosynthetic route from acetyl-CoA to steroidal glycoalkaloids, including additional related pathways that utilize the same substrate. Dashed arrows represent multiple enzymatic steps. The term "terpenes" refers to low-molecular-weight isoprenoids; Panel (b) shows the chemical structures of several intermediates involved in SGA biosynthesis. Abbreviations are as follows: HMGR, 3-hydroxy-3-methylglutaryl coenzyme A reductase; SS, squalene synthase; VSP, vetispiradiene cyclase; SMT, sterol C24-methyltransferase; and SGT, solanidine glycosyltransferase (Ginzberg et al., 2009).

2.8 Neurotoxicity of a-Solanine

Absorption of solanine through the gastrointestinal tract is less likely and accumulates in the highest concentration in the spleen and lower concentrations in the kidney, liver, lung, fat, heart, brain, and blood. Extreme consumption affects the nervous system because it inhibits the action of acetylcholinesterase in vivo and in vitro studies (Figure 4) (Garcia et al., 2015).

The glycoalkaloid sugar fraction is broken down during the uptake process, allowing the aglycone to be absorbed, which has been associated with adverse effects on the nervous system (Figure 2) (Uluwaduge, 2018). Clinical features of solanine poisoning include gastrointestinal and neurological symptoms. Typically, these symptoms appear 8 to 12 h post-injection, although they may appear as soon as 30 min after the consumption of high levels of solanine (Smith et al., 2008). Two closely related enzymes expressed in humans, acetylcholinesterase (AChE; E.C. 3.1.1.7) and butyrylcholinesterase (BuChE; acylcholine acylhydrolase; pseudocholinesterase; E.C. 3.1.1.8), play critical roles in cholinergic transmission. AChE is responsible for terminating cholinergic transmission at the neuromuscular junction and in the central nervous system. This enzyme is also a target for numerous inhibitors that are important in medical therapy and toxicology (Çavdar et al., 2019). Solanaceous glycoalkaloids (SGAs), which are naturally found in plants of the *Solanaceae* family such as potatoes, inhibit the activities of BuChE and AChE. α-Solanine and α-chaconine are the major SGAs in potato that have caused concern for human health due to their inhibition of both AChE and BuChE (Popova et al., 2022). Although steroidal glycoalkaloids have anticancerogenic properties in small amounts, compared to their beneficial properties, they have toxic effects on humans and cause poisoning and symptoms such as vomiting or diarrhea (Baur et al., 2021).

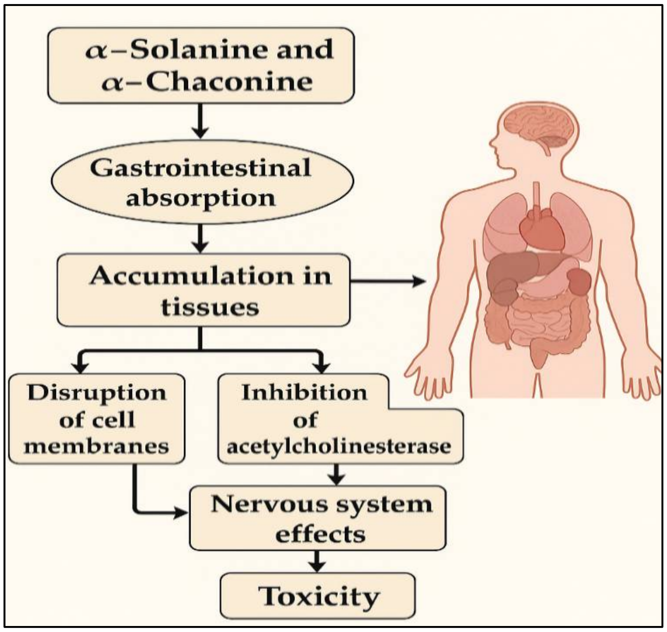

Figure 4. Proposed mechanism of a-solanine and a-chaconine toxicity in humans. *Image generated using artificial intelligence (ChatGPT/DALL·E, OpenAI) based on scientific literature.*

2.9 Thermal and Chemical Stability of Glycoalkaloids in Potatoes: Effects of Common Cooking Methods and Pre-treatment Strategies

Home processing, such as baking, boiling, frying, and microwaving has little effect on the reduction of glycoalkaloids in potatoes. There are also reports about the stability of glycoalkaloids during potato processing and the presence of these compounds in the final products (Omayio et al., 2016). These reports show that processing potatoes to potato flakes diminished the content of glycoalkaloids, mainly due to peeling and leaching, but thermal exposure had a less significant influence (Mäder et al., 2009). In addition, in the research conducted by Nie et al. (2018), it was shown that the processing of French fries significantly reduces the glycoalkaloid content in the final product compared to the raw material. Nevertheless, several studies have demonstrated that peeling is a highly effective method, eliminating up to 50% of the glycoalkaloids that are primarily concentrated in the potato skin. Furthermore, boiling peeled potatoes can significantly reduce α-solanine levels by as much as 80% and α-chaconine by up to 65% through leaching. Frying at 210°C for 10 min results in a substantial reduction of glycoalkaloids, with decreases of up to 90% due to thermal degradation. In contrast, microwaving is less efficient, with a reduction of approximately 15% in glycoalkaloid content (Mäder et al., 2009). A study conducted in 2020 demonstrated that pre-treatment of potatoes with organic acids-such as acetic, citric, lactic, and malic acids-can significantly reduce glycoalkaloid content. Notably, soaking potato tubers in a 1% acetic acid solution for eight hours resulted in a reduction of more than 90% in both α-solanine and α-chaconine concentrations (Liu et al., 2020).

2.10 Control of glycoalkaloid formation in potato

Glycoalkaloid formation can have serious economic losses for the producer, distributor, and consumer. Therefore, it is recommended that adequate and diverse methods be available to delay or minimize glycoalkaloid formation. At this point, some of the methods that have been studied will be discussed.

2.11 Genetics

Based on the studies, none of the commercial potato varieties are completely devoid of glycoalkaloids, and the amount of glycoalkaloid content can be different under the influence of potato variety. Therefore, many efforts have been made to breed potato varieties with very low glycoalkaloid levels. Based on research conducted in 2002 in Italy, it was shown that non-conventional breeding approaches, such as somatic fusion and sexual hybridization, can lead to the improvement of potato varieties with lower glycoalkaloid levels (Esposito et al., 2002). In the study conducted by Urban et al. (2018), it was shown that the genotype of potato cultivars has a decisive effect on glycoalkaloid content, so that some cultivars have lower levels and others have higher levels. Also, researchers evaluated the definitive and determining effect of genotype on glycoalkaloid content, so that in the research conducted by Sánchez del Pulgar et al. (2021) on potato clones, it was shown that genotypic variation is the main factor affecting glycoalkaloid accumulation.

2.12 Packaging

In a study, researchers used modified packaging atmosphere with carbon dioxide and ozone in order to control glycoalkaloid synthesis and showed that with an increase in the CO_2 exposure, glycoalkaloid concentrations decreased, yielding improved quality (Vorne et al., 2002). Also, Gang evaluated the changes in greening rate and glycoalkaloid content of potatoes packed in colored polyethylene (PE) bags during storage in conditions of 18 to 22 °C, 40 to 60% relative humidity, and uniform and mild natural light. The results showed that under natural light conditions, the greening rate and glycoalkaloid content of the control potato increased rapidly with long storage time. Meanwhile, polythene bags with different colors, especially black and green bags, effectively prevent greening and increase glycoalkaloid content in stored potatoes (Gang, 2010).

2.13 The use of chemicals in inhibiting the synthesis of glycoalkaloids

Extensive research has been conducted using a wide range of chemicals and methods to control glycoalkaloid formation. El-Said (2013) showed that the use of compounds containing sulfur can lead to a decrease in the content of toxic glycoalkaloids in potato tubers. Due to having free sulfhydryl groups, these compounds directly affect glycoalkaloids in order to reduce their toxicity. In this study, garlic bulbs and sodium bicarbonate were added to potatoes as a safe source of sulfur, and based on the results, the content of glycoalkaloids in peeled potato tubers under garlic treatment was reduced to 85-90% compared to the level of glycoalkaloids before treatment. Meanwhile, the potato/garlic/sodium bicarbonate mixture had the lowest amount of total glycoalkaloid (10.455 mg/kg) in 120 min at 90°C and pH 8. Mystkowska (2019) found that the use of biostimulators such as biostimulator BrunatneBio Złoto Cytokinin, GreenOk, Kelpak SL, Titanit, can also lead to a significant reduction of glycoalkaloid content in the leaves and tubers of potato varieties. However, the widespread use of agricultural chemicals has raised health concerns.

2.14 Application of Green Technologies to Prevent Toxin Formation or Promote Breakdown in Potatoes

Green technologies represent a transformative approach to modern agriculture, offering innovative solutions to boost productivity while prioritizing environmental sustainability. These advancements focus on reducing ecological impact, optimizing resource use, and enhancing food security. They aim to cut water and energy consumption, improve pest and disease management, enrich soil quality, and curtail greenhouse gas emissions. In the realm of crop cultivation, particularly for potatoes-a staple and globally significant food source-green technologies have proven indispensable. These methods tackle critical challenges such as controlling natural toxins like glycoalkaloids, improving storage efficiency, and cultivating resilient, low-toxin potato varieties. Cutting-edge techniques, including gene editing tools like CRISPR-Cas9, microbial biotechnologies, and nanotechnology applications, effectively mitigate toxin levels and enhance breakdown processes. Such strategies not only ensure the production of safer, higher-quality potatoes but also significantly lower the environmental impact of farming (del Mar Martínez-Prada et al., 2021).

2.15 Genetic Engineering

Advancements in genetic engineering have paved the way for the development of potato varieties with significantly lower levels of glycoalkaloids. Techniques like CRISPR-Cas9 and RNA interference (RNAi) are being utilized to specifically target genes involved in the synthesis of these compounds (del Mar Martínez-Prada et al., 2021).

A 2009 study by Ginzberg highlighted the potential of transgenic technologies, including the application of the SMT1 gene and antisense constructs targeting glycosylation-related genes, as effective tools for minimizing tuber toxicity. By lowering both total and specific glycoalkaloid levels, these approaches could lead to the development of potatoes with safer tubers and optimized SGA profiles, all while maintaining the plant′s inherent defenses against pests and diseases. Advancing our understanding of SGA-related genes and refining breeding strategies offers a promising pathway toward the production of safer and more functional food crops (Ginzberg et al., 2009).

By targeting genes involved in the breakdown of SGAs, it is possible to transform these compounds into non-toxic, non-bitter forms. For instance, the enzymes hydroxylase GAME31/23DOX and glycosyltransferase GAME5, along with other yet-to-be-identified enzymes, can convert α-tomatine, an SGA present in immature tomatoes, into harmless substances, thus eliminating bitterness and toxicity from the ripe fruit. Additionally, silencing the DR2-7 gene in tomatoes reduces α-tomatine levels while increasing provitamin D3 without any detrimental effects on the plant. Considering the similarities in the biosynthetic pathways and regulatory mechanisms of SGA production in both potato and tomato, the metabolic processes of SGAs in tomatoes offer valuable insights that could aid in the transformation of SGAs in potatoes into non-toxic compounds (Ginzberg et al., 2009).

2.16 Controlled Storage Conditions

Proper storage techniques are a sustainable approach to minimizing glycoalkaloid formation. Storing potatoes in cool, dark environments prevents exposure to light and delays the greening process that induces solanine production. A study by Kozukue and Mizuno (1990) highlighted that maintaining storage temperatures between 7 to 10°C and relative humidity of 85-90% significantly reduced toxin levels in stored potatoes. Additionally, using UV-blocking packaging materials has been shown to prevent glycoalkaloid synthesis caused by light exposure.

2.17 Post-Harvest Treatments

Post-harvest interventions, such as washing, peeling, and sprout removal, can decrease glycoalkaloid concentrations. Since these toxins are primarily located in the skin and sprouts, removing these parts diminishes the risk of ingestion. Research by Muñoa et al. (2022) demonstrated that mechanical peeling reduced glycoalkaloid levels by 50-70%, while thermal blanching eliminated residual toxins on the surface. Also, boiling and frying methods have been studied, with boiling reducing glycoalkaloid content by approximately 30%. However, frying can lead to the concentration of toxins if temperatures exceed safe thresholds.

Two separate studies, published in 1996 and 2020, examined how both selective breeding and mutation breeding can help reduce the concentration of toxic glycoalkaloids in potatoes. Over generations of domestication, selective breeding for varieties with milder taste has naturally lowered glycoalkaloid levels in tubers; levels that can reach up to 3,500 mg/kg in wild relatives have been substantially reduced in modern cultivars. On the other hand, the 1996 study demonstrated that exposing the NDA1725-1 clone to gamma radiation successfully yielded three mutant lines with lower glycoalkaloid content across six clonal generations, without compromising essential agronomic traits. In both breeding approaches, glycoalkaloid levels were a central factor in the selection process, underscoring their role in food safety. Collectively, these results highlight the value of both traditional and mutation-based breeding as practical tools for developing safer potato varieties. A combined strategy may offer even greater potential for enhancing both the safety and quality of this globally important crop (Love et al., 1996; Kaiser et al., 2020).

2.18 Microbial Treatments

A study by Song et al. (2023) explored the use of the endophytic bacterium *Alkalihalobacillus clausii PA21* as an innovative strategy to reduce toxic glycoalkaloids in potatoes. Under controlled lab conditions, the bacterium demonstrated impressive degradation capabilities, breaking down over 91% of α-solanine and more than 93% of α-chaconine. When applied to stored potato tubers, it also achieved a substantial reduction in α-solanine levels-nearly 68% compared to untreated controls. Notably, this decline had no adverse effects on key nutritional elements such as starch, vitamin C, or protein. The treatment also appeared to reshape the tuber′s internal microbial community in ways that may help limit future toxin buildup. Taken together, the results point to microbial intervention as a promising, eco-friendly alternative to conventional chemical methods for improving potato safety.

2.19 Nanotechnology Applications

A 2018 study explored the potential of hydrophobic nanosilica as a novel tool for managing sprouting and lowering glycoalkaloid levels in stored potatoes. The application of this nanoscale coating was found to be effective in not only suppressing sprout growth over time but also in significantly reducing α-solanine concentrations. Researchers attributed these effects to limited light and oxygen exposure, along with modified gas exchange at the tuber surface. Unlike conventional chemical inhibitors, this nanotechnology-based method offered a cleaner, more sustainable solution without compromising the nutritional or sensory quality of the potatoes. As a result, nanosilica emerges as a promising alternative with fewer environmental and health risks. Overall, the study underscores the valuable role nanotechnology could play in enhancing food safety and extending storage life (Zhang et al., 2018).

2.20 Potato glycoalkaloid analysis methods

Recently, various methods and devices have been widely used to detect solanine in products such as potatoes, tomatoes, and eggplants, which are time-consuming, tedious, expensive, and destructive (Dokhani et al., 2003).

Another method of measuring glycoalkaloids is the colorimetric method. Reagent mixtures used in this method include sulfuric acid and formaldehyde (Marquis Reagent), phosphoric acid and paraformaldehyde (Clark's reagent), and antimony chloride/hydrochloric acid. The colorimetric method has high accuracy in quantitative diagnosis, but limitations in cost, corrosiveness, and toxicity, reactivity with steroids if present in the analyzed extracts, destruction of samples, and also environmental pollution are disadvantages of using the chemical reagent method (Lu et al., 2019). After that, thin layer chromatography (TLC), gas chromatography, spectrophotometry, and enzyme methods were used, in which the extracted glycoalkaloids are permethylated before analysis, and each had its shortcomings (Babazadeh et al., 2020). One of the main advantages of this method is the theoretical separation of α, β, and γ forms of chaconine and solanine as well as solanidine (Dokhani et al., 2003).

High-performance liquid chromatography with ultraviolet detector (HPLC-UV), or tandem mass spectrometry detector (LC-MS/MS), immunochemical methods such as Enzyme Linked Immunosorbent Assay (ELISA) and enzyme immunoassay (EIA), capillary electrophoresis, and biosensors are other methods used to measure glycoalkaloids in products such as raw or processed potatoes (Liu et al., 2014; Skarkova et al., 2008). Therefore, it is vital to use accurate, fast, reliable, efficient, and non-invasive alternatives to evaluate the characteristics related to the quantity and quality of food products. In 1986, Bushway and Perkins used the HPLC method for the first time, which had advantages over previous methods, such as complete separation of glycoalkaloids from each other and faster testing. Ultra-performance liquid chromatography (UPLC) is another developed technique that is commonly used for the separation of glycoalkaloids and has many advantages over its predecessor (Baur et al., 2021). The fluorescence hyperspectral image method reported by Lu et al. (2019) to measure solanine content in potatoes is another modern and developed technique in the field of microanalysis, which has non-destructive effects on the product and, on the other hand, has a higher sensitivity than It has colorimetric and spectrophotometric methods. Also, the use of optical sensors has been evaluated as a potential tool in several studies due to their non-destructive effects on food safety (Babazadeh et al., 2020). This technique, called laser-induced light backscattering imaging, focuses on image processing by digital cameras in the visible and short near-infrared (NIR) wavelengths of the electromagnetic spectrum (Babazadeh et al., 2016).

3. Conclusion

Glycoalkaloids in potatoes are believed to have naturally developed as a means for the plant to defend itself against harmful pathogens and challenging environmental conditions. Research indicates that elements such as the method of cultivation, periods of drought, and how the potatoes are stored after harvest can significantly influence the formation and build-up of these toxic substances in the tubers. Because their toxicity is closely linked to specific exposure conditions, it's crucial to maintain proper storage environments. Adopting eco-friendly approaches-like genetic modification, selective breeding, microbial techniques, and nanotechnology-shows strong potential in either minimizing or breaking down these harmful compounds. Enhancing storage systems and integrating such technologies can not only make potatoes safer to eat but also help curb food waste and lessen environmental harm. Additionally, exploring the possible health benefits of glycoalkaloids, particularly their disease-fighting and antimicrobial properties, could open new doors for their use in medical and nutritional science.

Authors' Contributions

Mina Saei, Naiema Vakili Saatloo, Parisa Shavali-gilani, Nastaran Akbariyeh, Fatemeh Cheraghian, Leila Haji: Methodology; Writing original draft; review & editing. **Parisa Sadighara:** Conceptualization; Project administration; Supervision; Validation; Methodology; Writing original draft; review & editing. **Tayebeh Zeinali:** Conceptualization; Project administration; Supervision; Validation; Methodology; Writing original draft; review & editing.

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Conflicts of Interest

The authors declare that they have no conflict of interest.

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Ethical considerations

There were no ethical considerations to be considered in this research.

Using Artificial Intelligence

The authors declare that AI tool used for the image designation, editing and revising of this paper.

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