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Glycoalkaloids in Potato: A Comprehensive Overview of Accumulation, Detection and Mitigation Strategies

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Abstract

Glycoalkaloids are bioactive secondary metabolites predominantly found in Solanaceae species, which are known for their dual role as natural defence compounds and potential toxicants for human and animal consumption. Accurate analysis of glycoalkaloids is, therefore, of crucial importance for food safety, agricultural practice and pharmaceutical research. This review highlights how different factors, including genetic variation, extraction methods and analytical techniques, contribute to differences in the analysis of glycoalkaloids. It provides a comparative analysis of the different analytical methods used for the detection and quantification of glycoalkaloids. These range from traditional techniques, such as coulometric methods and enzyme-linked immunosorbent assay (ELISA), to more advanced approaches, including high-performance liquid chromatography (HPLC) and liquid chromatography-mass spectrometry (LC–MS). This review discusses the challenges in analysing glycoalkaloids, including difficulties in extraction, interference with matrix components and the need for standardised methods. Furthermore, emphasis is placed on the significance of glycoalkaloid analysis in domains such as food safety, agriculture and medicine, particularly highlighting their role in plant breeding, toxicology, and therapeutic potential. Finally, emerging trends in glycoalkaloid analysis, such as innovative technologies and data-driven approaches, are examined to improve detection sensitivity and efficiency. This review underscores the necessity of comprehending the factors that influence glycoalkaloid analysis to ensure food safety and to advance scientific research.

Keywords α-Chaconine · α-Solanine · Analytical methods · Detection sensitivity · Food safety · *Solanum tuberosum* L.

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Introduction

Potato (*Solanum tuberosum* L.) is one of the most widely cultivated and consumed crops worldwide and plays an important role in food security and human nutrition (Haase 2010). Its adaptability to different climatic conditions, high yield potential and rich nutritional profile make it an important part of the diet in different cultures. In addition to its role for human consumption, potato also serves as a valuable raw material for the food industry and as animal feed, which further emphasises its agricultural and economic importance (Ierna and Distefano 2024). However, despite its nutritional and economic importance, potato naturally contains bioactive compounds known as glycoalkaloids (GAs), which can pose potential health risks in high concentrations (Al Sinani and Eltayeb 2017). While GAs contribute to plant defence mechanisms, they also have a dual nature: at low concentrations, they possess beneficial biological properties, including antimicrobial (Sołtys-Kalina et al. 2023; Liu et al. 2020; Ismail et al. 2019; Dahlin et al. 2017), anticancer, and pharmacological activities (Patel et al. 2021; Friedman 2015). Conversely, excessive accumulation of GAs can lead to adverse health effects in humans and animals, causing gastrointestinal disturbances, neurological disorders, and, in severe cases, toxicity (Ahamad et al. 2022). This complex balance underlines the need for accurate quantification and characterisation of GAs, both to ensure food safety and to explore their potential therapeutic applications. Among the GAs present in potato, α-solanine and α-chaconine are the most abundant and biologically active (Omayio et al. 2016; Devkota et al. 2015; Friedman 2006). These compounds are mainly concentrated in the tubers, peels and leaves, where they contribute to the plant's natural defence mechanisms against pests and diseases (Kuc 1984; Tingey 1984). However, when their concentration exceeds safety thresholds, they pose a significant health risk, especially to consumers, necessitating strict food safety regulations (Nara et al. 2019; Ruprich et al. 2009). Factors such as variety, environmental conditions and post-harvest treatment can strongly influence GA accumulation, leading to significant differences in concentration between potato varieties (Haase 2010; Knuthsen et al. 2009; Fitzpatrick et al. 1978). In particular, exposure to light can significantly increase the GA concentration, sometimes by a factor of 2 to 3, which increases the risk of toxicity (Rymuza et al. 2020; Mekapogu et al. 2016; Machado et al. 2007; Salunkhe et al. 1972). Although thermal processing methods are widely used in food preparation, their ability to degrade GAs is limited. Conventional cooking methods such as boiling and microwave heating generally reduce the GA content by only 4–6% and 10–15%, respectively (Guruprasad et al. 2024). High-temperature methods such as frying and baking also show minimal reduction as α-solanine and α-chaconine are very heat stable (Lachman et al. 2013; Tajner-Czopek et al. 2012; Finotti et al. 2006). Given this resistance to degradation, appropriate post-harvest handling, storage and processing conditions are crucial to minimising the accumulation of GA in food and thus reducing potential health risks (Schrenk et al. 2020).

High-performance liquid chromatography (HPLC) has established itself as the gold standard for the qualitative and quantitative analysis of GAs. This technique offers superior sensitivity, precision and separation efficiency, making it ideal for

the detection and profiling of GAs in plant tissues, food, and biological samples (Wolfender et al. 2018). Compared to conventional methods, HPLC offers unrivalled resolution and reproducibility with the added flexibility of different detection systems such as ultraviolet (UV), fluorescence, and mass spectrometry (MS) (Donno et al. 2020; Skrabule et al. 2013). However, there are still challenges in GA detection, particularly in relation to the variability of extraction yields, which can be influenced by factors such as the plant part used, environmental conditions, and sample preparation techniques (Topolewska and Haliński. 2024; Devkota et al. 2015). Furthermore, the lack of standardised extraction protocols has led to inconsistent results in different studies. Conventional extraction methods often suffer from low selectivity and co-extract impurities that complicate subsequent chromatographic analysis and require further purification (Bitwell et al. 2023). Although advanced techniques such as HPLC are effective for quantification, they cannot detect low concentrations of GAs, which can underestimate their presence in food (Lyu et al. 2020; Larcher and Nardin 2019; Knuthsen et al. 2009). From an industrial perspective, many laboratory-scale extraction methods are not scalable and require expensive reagents or specialised equipment, making them economically impractical for large-scale food safety monitoring (Benkeblia 2020; Elżbieta 2012; Alt et al. 2005). In addition, the environmental impact of using organic solvents in conventional extraction methods necessitates the development of more environmentally friendly alternatives that minimise solvent waste and reduce energy consumption (Bouhzam et al. 2024; Cheriyan et al. 2024; Clarke et al. 2018). A notable gap in current research is the lack of systematic comparative studies evaluating extraction methods for different plant matrices and environmental conditions. Moreover, longitudinal research examining how agricultural practices and environmental factors influence GA accumulation over time remains limited.

The complexity of GA toxicity requires a multidisciplinary approach involving collaboration between food scientists, toxicologists, and plant biologists. This collaboration could improve risk assessment methodologies and lead to a deeper understanding of GA metabolism, thus helping to mitigate risks to human health. The introduction of standardised testing protocols and the development of comprehensive databases would enable more consistent comparisons between studies, supporting the development of guidelines and safety assessments. Future research in this area should focus on optimising extraction protocols, improving detection techniques and exploring sustainable alternatives to current methods to ultimately improve food safety and protect public health.

The objective of this review is to provide a focused and critical synthesis of current knowledge on glycoalkaloids (GAs) in *Solanum tuberosum*, with particular emphasis on their implications for food safety and quality. Specifically, the review addresses three major thematic areas. First, it examines the genetic and environmental factors that regulate the biosynthesis and accumulation of GAs in potato tubers, including both constitutive mechanisms and stress-induced responses. Second, it evaluates the range of analytical methodologies employed for the extraction and quantification of glycoalkaloids - particularly α-solanine and α-chaconine - with an emphasis on chromatographic and spectrometric techniques and their applicability in both research and regulatory

settings. Third, it explores current mitigation strategies aimed at reducing GA content along the production and processing chain, including agronomic practices, postharvest handling, thermal processing and breeding approaches. Through this integrative lens, the review aims to consolidate dispersed knowledge, identify persistent gaps and support the development of scientifically informed strategies to manage glycoalkaloid levels in the potato value chain.

Approach to Literature Selection

A methodological approach was employed to guide the selection of literature. The objective was to ensure comprehensive coverage of key scientific contributions across the domains of plant secondary metabolism, food safety, analytical chemistry, and crop improvement, all relevant to the study of glycoalkaloids in *Solanum tuberosum*. The literature search was conducted using three principal academic databases—PubMed, Scopus, and Google Scholar—chosen for their extensive and complementary coverage of biomedical, agricultural, and interdisciplinary research. Search queries were constructed using Boolean operators to combine core keywords such as "glycoalkaloids", "α-solanine", "α-chaconine", "potato", "biosynthesis", "stress response", "cold storage", "light exposure", "HPLC", "LC–MS", "quantification", "toxicity", "processing", and "breeding".

The inclusion criteria encompassed (i) peer-reviewed primary research articles, reviews, and authoritative book chapters; (ii) publications in the English language; and (iii) studies explicitly addressing the accumulation, detection, mitigation or toxicological relevance of glycoalkaloids in potato. The temporal scope of the search spanned from 1960 to 2025, with deliberate emphasis on significant advances published in the last two decades. While the review prioritises recent advances, key studies published prior to 2000 were also included when they provided foundational insights into glycoalkaloid biosynthesis, toxicity or analytical methodologies. We also utilised Connected Papers (http://www.connectedpapers.com), a graph-based literature discovery tool that enables the visualisation of co-citation networks and thematic proximities among publications. This exploratory layer was instrumental in identifying conceptually relevant, high-impact contributions that might elude conventional keyword-based retrieval. It also helped in mapping the structural logic of the review around three principal axes: factors influencing glycoalkaloid accumulation, analytical methods for their quantification and mitigation strategies spanning the production and processing continuum. This integrative and multi-source approach was designed to ensure both the breadth and depth of the review, while enhancing its scholarly coherence and relevance to multidisciplinary readerships engaged in potato research, food quality control, and phytochemical risk assessment.

Factors Influencing Glycoalkaloid Accumulation

The accumulation of GAs in potato is influenced by a combination of genetic, environmental, and agronomic factors. Genotypic variations play a crucial role, as different potato varieties have different levels of GA biosynthesis, with some naturally producing higher concentrations. Environmental stressors such as drought, extreme temperatures, and pest infestations can trigger the plant's defence mechanisms, leading to increased GA synthesis. In addition, mechanical damage during harvest and storage in response to wounds can stimulate GA production (Fitzpatrick et al. 1978). Agronomic practices, including excessive nitrogen fertilisation and prolonged exposure to light, also contribute to increased GA concentrations (Nguyen et al. 2024; Zhang et al. 2020; Şengül et al. 2004; Kuc 1984; Nowacki et al. 1975). Understanding these factors is crucial for the development of effective mitigation strategies through breeding, optimised cultivation techniques and improved storage conditions (Fig. 1).

Genetic Effect in Glycoalkaloid Accumulation

While the role of GAs as natural defences is well recognised, their variability—particularly between wild and cultivated varieties—represents both an opportunity and a challenge for breeding programmes to improve food safety (Osman et al. 1978). Wild potato species generally have a significantly higher GA content than their cultivated counterparts (Savarese et al. 2009; Kozukue et al. 2008). This difference is largely attributed to evolutionary pressures that have shaped wild species to survive under high biotic stress, where robust chemical defences are essential. For example,

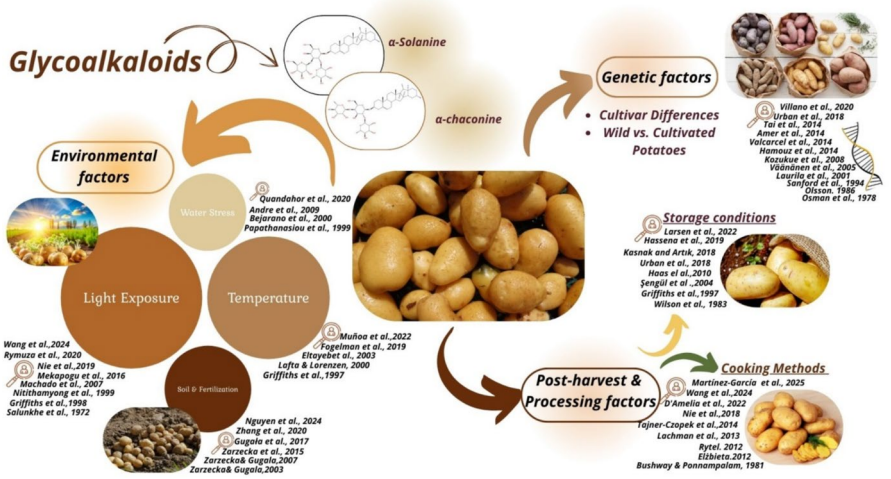

Fig. 1 Mind-mapping of factors influencing the accumulation glycoalkaloids in potato and relevant references to support these findings

Villano et al. (2020) have identified key HMG genes, with ScHMG1 being a key regulator in *Solanum commersonii*. Overexpression of this gene leads to significantly increased GA biosynthesis, demonstrating a clear genetic mechanism that supports natural defence in wild species. These results reinforce the concept that the genetic architecture of GA accumulation is fundamentally linked to survival strategies in the natural environment (Ginzberg et al. 2009). Conversely, cultivated varieties have been selectively bred to favour traits such as palatability and lower toxicity, resulting in generally lower GA concentrations. Nevertheless, there are still considerable differences between commercial varieties (Olsson 1989). For example, studies by Martínez-García et al. (2024) and Aziz et al. (2012) report large differences in the concentrations of α-solanine and α-chaconine, suggesting that even within cultivated potato, genetic diversity plays a crucial role. This heterogeneity suggests that breeding practices have not fully homogenised GA content and that underlying genetic variability persists, offering both potential benefits and risks in terms of plant resilience and consumer safety.

The integration of wild species into breeding programmes is a double-edged sword (Nicolao et al. 2023). On the one hand, wild relatives provide valuable traits such as pest and disease resistance. On the other hand, their naturally high GA content can be inadvertently introduced into hybrids, complicating food safety assessment (Savarese et al. 2009). The emergence of novel GA profiles in interspecific hybrids, as reported by Väänänen et al. (2005) and Laurila et al. (1996), further complicates this problem. These hybrids can produce GAs that are not present in either parental line, and the toxicological profiles of these new compounds are often poorly understood (Laurila et al. 2001). This emphasises the need for rigorous biochemical screening and genetic analysis when including wild germplasm to ensure that improved resistance properties do not come at the expense of increased toxicity.

Apart from inherent genetic differences, developmental stages such as sprouting can also modulate GA content. Driedger et al. (2000) demonstrated that sprouted tubers have significantly higher GA concentrations compared to non-sprouted tubers, emphasising the dynamic nature of GA biosynthesis in response to physiological changes. In addition, tuber pigmentation appears to correlate with GA content (Hamouz et al. 2014). Studies by Urban et al. (2018) and Tajner-Czopek et al. (2014) show that red and purple-fleshed varieties tend to have higher GA contents compared to white-fleshed varieties. This suggests that certain phenotypic traits, possibly linked to common metabolic pathways with anthocyanin synthesis, may influence GA biosynthesis, adding another layer of complexity to the genetic regulation of these compounds (Jansen and Flamme 2006). It is also important to note that the variability in reported GA concentrations may be due to different sampling strategies and analytical methods. For example, studies using leaflets or whole foliage have produced different results, as highlighted by Sanford et al. (1994) and Tai et al. (2014). Harmonisation of these methodologies is essential to obtaining consistent and reliable data, especially when it comes to drawing conclusions about the genetic control of GA biosynthesis. For the future, an integrated approach combining genomic analysis with advanced biochemical screening is required (Al Aboud 2024). Such an approach would allow researchers to decipher the precise genetic pathways involved in GA biosynthesis and regulation, while monitoring the effects

of environmental and developmental factors (Umemoto et al. 2016). Ultimately, this could lead to the development of potato varieties that optimise beneficial traits such as pest resistance while minimising the risks associated with high GA content.

Environmental Factors

Although genotype is recognised as the primary determinant, it is crucial to acknowledge that environmental conditions also significantly influence GA content, often leading to variation from year to year and between different potato varieties (Urban et al. 2018). This section evaluates the various environmental factors that influence GA synthesis, such as light exposure, temperature, water stress, and agronomic practices, emphasising the need for an integrated understanding of these factors to improve potato quality and safety.

Light is a key environmental cue in plant development, particularly influencing secondary metabolism in *Solanum tuberosum* and the biosynthesis of GAs (Machado et al. 2007). A growing body of evidence underscores that light intensity, duration and spectral quality significantly affect GA accumulation, with distinct responses depending on these factors (Sotelo and Serrano 2000; Friedman 2006). Nitithamyong et al. (1999) reported that moderate light intensity (< 500 μmol•m^{-2}•s^{-1}) promotes GA accumulation, while excessive intensity (> 750 μmol•m^{-2}•s^{-1}) causes a decline due to photoinhibition or oxidative stress, limiting metabolic flux. These findings suggest that potato exhibits a parabolic response to light intensity, with an optimal range for GA biosynthesis. Red light, in particular, has been identified as the most effective wavelength for inducing glycoalkaloid biosynthesis, leading to accelerated and higher levels of accumulation compared to other wavelengths (Okamoto et al. 2020). α-Chaconine, the more predominant GA, is typically synthesised in greater quantities than α-solanine, which may reflect differential gene regulatory mechanisms or enzyme activities along the GA biosynthetic pathway. Notably, light exposure does not only modulate gene expression but can also influence chromatin structure, an emerging area in plant secondary metabolism. Red light exposure induces DNA demethylation, thereby increasing solanine accumulation, suggesting that light-mediated epigenetic changes play a role in activating key biosynthetic genes (Xiong et al. 2022). At the molecular level, these processes are mediated by phytochrome photoreceptors—StPHYA, StPHYB, StPHYC, and StPHYE—which function as light sensors, particularly in the red/far-red spectrum. Transcriptome analysis has shown that red and white light exposure significantly upregulates the expression of StPHYB, StPHYC, and StPHYE, which correlate with enhanced GA accumulation (Zhang et al. 2023). This connection points to the involvement of phytochrome signalling pathways in regulating GA biosynthesis. However, while these correlations are evident, the precise mechanistic links between phytochrome signalling and transcriptional activation of glycoalkaloid biosynthetic pathways remain unclear. Further research is necessary to elucidate whether phytochromes directly activate biosynthetic genes or whether intermediary transcription factors and chromatin modifications mediate this process. In addition to light intensity and spectral quality, light exposure also interacts with other environmental factors, such

as temperature and day length. Longer light exposure times and increased photosynthetic photon flux (PPF) have been shown to elevate GA content, as evidenced by studies on variety-specific responses. For example, the varieties Lord and Irga exhibit variable GA accumulation, with longer exposure to light leading to higher GA levels (Rymuza et al. 2020). This variation highlights the need for tailored light management strategies that consider the specific requirements of different potato varieties to control GA biosynthesis during the growth phase.

Temperature plays a central role in GA biosynthesis (Şengül et al. 2004). Studies have shown that high temperatures lead to increased GA concentrations in potato tubers. Eltayeb et al. (2003) and Muñoa et al. (2022) observed that tubers exposed to temperatures above 30 °C had significantly higher GA concentrations, which may exceed the safety thresholds for human consumption. Above all, the potato genotype plays a decisive role in the reaction to temperature stress. Some varieties are more resistant to heat stress and produce lower GA concentrations even at higher temperatures, while others are more susceptible (Fogelman et al. 2019). This genotype-specific variability provides opportunities for breeding programmes aimed at developing heat-tolerant potato varieties with reduced GA content (Dempewolf et al. 2014). However, it is important to note that the relationship between temperature and GA accumulation is complex. High temperatures do not always lead to increased content. In some cases, heat stress has been shown to reduce the synthesis of certain secondary metabolites, including GAs (Fogelman et al. 2019).

Water stress, especially drought, is another crucial factor influencing GA accumulation in potato. Drought-induced oxidative stress is thought to trigger the production of reactive oxygen species (ROS), which activate defence mechanisms that include the biosynthesis of secondary metabolites such as GAs (Andre et al. 2009). Research by Yadav et al. (2021) suggests that phytohormones such as abscisic acid (ABA) and salicylic acid (SA) can modulate the synthesis of GAs under drought stress. ABA is known to regulate the plant's response to water deficit, while SA has been implicated in defence responses to oxidative stress (Khan 2025; Li et al. 2022). Despite these findings, the genetic and enzymatic pathways that regulate GA accumulation under water stress remain unclear. Empirical studies have demonstrated a direct correlation between drought and increased GA concentration in potato tubers (Quandahor et al. 2020). However, the effect of drought on GA accumulation is very variety-dependent. For example, the British Queen variety shows a significant increase in GA content when exposed to both drought and waterlogging, while other varieties such as Desiree show a more modest response (Bejarano et al. 2000; Papathanasiou et al. 1999). This variability emphasises the importance of considering genotype when assessing the effects of drought on GA content. In addition, the conflicting results of studies investigating the effects of flooding on GA synthesis add complexity to the understanding of water stress. Peivastegan et al. (2019) found that flooding led to downregulation of key genes involved in GA biosynthesis, suggesting that flooding can reduce GA content. This contrasts with the typical response to drought stress and raises important questions about the differential effects of water stress on GA synthesis.

Research on potato GAs has evolved considerably, highlighting the interplay between agricultural practices, environmental conditions, and biochemical

processes. Studies suggest that factors such as rainfall, soil erosion and vine removal methods influence GA synthesis. Merino et al. (2023) found that mechanical removal of vines combined with insufficient tillage increased soil erosion, exposed tubers to daylight and stimulated solanine accumulation, especially in light-sensitive varieties. The use of herbicides, particularly Sencor 70 WG and Basagran 600 SL, has been shown to increase ascorbic acid content in potato without significantly altering glycoalkaloid content (Zarzecka and Gugala 2003). In the study of Gugała et al. (2017), the application of the soil conditioner UG_{max} significantly influenced the GA content in potato tubers. The highest concentration of GAs was observed when UG_{max} was applied prior to planting, followed by an additional application at the potato plants height of 10–15 cm and at the flower bud stage. This treatment combination resulted in the highest levels of GAs, highlighting the impact of UG_{max} on enhancing their content in the tubers. However, the long-term effects of these agronomic practices on potato biochemistry remain unclear. In addition, simplified tillage practices and herbicide use under hot, dry conditions have been shown to increase GA concentrations, further emphasising the role of environmental stress in GA synthesis (Zarzecka et al. 2015; Zarzecka and Gugala 2007). The synthesis and accumulation of GAs in potato is influenced by a variety of environmental factors, including light exposure, temperature, water stress and agronomic practices (Lafta and Lorenzen 2000). Although significant progress has been made in understanding the relationship between these factors and GA production, there are still some critical gaps. Future research should focus on elucidating the molecular pathways involved in GA biosynthesis, especially under different environmental conditions, and investigate how these pathways interact with other physiological processes. In addition, the genotype-specific response to environmental stressors needs to be considered when developing strategies to control GA content in potato. As climate change continues to alter weather patterns, it will be critical to identify potato varieties that can maintain safe levels of GAs under increasingly variable environmental conditions.

Post-harvest and Processing Factors

The storage conditions of potato have a significant influence on the accumulation of GAs, especially α-solanine and α-chaconine (Haase 2010). These compounds are concentrated in the peel, and improper storage can exacerbate their formation, leading to potential health risks. Environmental factors such as temperature, humidity, and exposure to light play an important role in regulating GA content.

Temperature is a decisive factor for the accumulation of GAs in potato. Studies by Lafta and Lorenzen (2000) and Urban et al. (2018) have shown that both temperature and humidity influence the concentration of GAs in stored tubers. Storage of potatoes at temperatures above 10 °C has been consistently associated with increased glycoalkaloid accumulation, particularly under conditions that promote sprouting and metabolic reactivation (Şengül et al. 2004). Elevated temperatures can stimulate the expression of genes involved in GA biosynthesis and compromise tuber dormancy, thereby intensifying the accumulation of α-solanine and

α-chaconine. For this reason, warm storage is generally discouraged for both commercial and domestic handling, especially in the absence of darkness or temperature regulation. Studies have shown that the GA content of potato under such conditions can increase by 15–30% in just 4 weeks due to light-induced chlorophyll production, which is directly linked to the formation of α-solanine and α-chaconine (Okamoto et al. 2020; Rytel et al. 2015; Griffiths et al. 1998). The influence of cold storage on glycoalkaloid (GA) accumulation in potato tubers is both multifaceted and cultivar-dependent (Şengül et al. 2004). Temperature plays a regulatory role not only during plant development but also throughout the postharvest phase, with outcomes shaped by a complex interplay of genetic, physiological and environmental factors. Moderate cold storage (typically 4–6 °C) under dark conditions has been reported to suppress GA biosynthesis by reducing enzymatic activity and limiting photomorphogenic signalling. For instance, Merino et al. (2023) observed no significant change in GA content after 6 months of dark storage in control tubers. In contrast, Griffiths et al. (1997) documented a marked increase in GA levels in Pentland Crown tubers stored at 4 °C over a short period, underscoring the pronounced sensitivity of certain cultivars to low-temperature stress. Moreover, storage outcomes can be further modulated by secondary stressors such as light exposure, mechanical damage and the initiation of sprouting—all of which can potentiate GA accumulation even under otherwise suppressive storage conditions. Compounding this, very low temperatures (< 4 °C) may also induce cold-induced sweetening, leading to elevated sugar levels that adversely affect processing quality (Colman et al. 2017). Taken together, these findings make clear that the relationship between cold storage and GA dynamics is not linear but governed by multiple interacting variables, including genotype, storage temperature, tuber physiological status, and duration (Kumar et al. 2004). As such, postharvest storage strategies must be carefully optimised to balance the suppression of GA biosynthesis with the preservation of overall tuber quality and safety.

Light exposure during post-harvest storage has profound effects on GA accumulation in potato, influencing the safety and quality of stored tubers (Machado et al. 2007). Exposure to light, particularly in the form of fluorescent or LED light, accelerates the greening process of potato, which is closely linked to increased GA concentrations. Larsen et al. (2019) showed that light exposure induced significant greening in potato tubers within 24 to 60 h, especially under LED light conditions at 20 °C. This rapid increase in GA content can render the tubers unmarketable and poses a potential health risk due to the toxicity of GAs. The detrimental effects of light exposure on GA accumulation underscore the importance of appropriate packaging solutions to limit light contact during storage, as well as temperature control, to minimise GA formation. The role of light in the storage phase is compounded by environmental factors such as temperature and humidity. For instance, Dhalsamant et al. (2022) reported that light exposure combined with improper storage conditions leads to unpredictable GA accumulation, especially in informal markets where storage practices are not regulated. The cumulative effect of light exposure during storage contributes to the increase in both α-chaconine and α-solanine levels, with significant implications for post-harvest quality (Wang et al. 2024). The mechanism driving this increase appears to be the continued activation of light-responsive genes, even after harvest. The photoreceptor activity of phytochromes in the tuber

cells may persist under light exposure, leading to the continued biosynthesis of GAs. Despite this, the challenge remains in finding effective packaging materials and strategies that can fully protect potato from light exposure during storage (Okamoto et al. 2020). Packaging solutions that block light effectively are crucial to controlling GA accumulation (Abbasi et al. 2016). However, research by Larsen et al. (2019) and others suggests that no packaging material can prevent light-induced greening for extended periods, especially under storage temperatures of 20 °C. Additionally, the interaction of light with other environmental factors, such as storage temperature, further complicates the regulation of GA levels. Ultimately, understanding the molecular mechanisms by which light exposure influences GA accumulation during storage will be critical in developing strategies to prevent light-induced toxicity in post-harvest potato tubers (Pinhero et al. 2009). Future research should explore how the persistence of light signalling pathways during storage might be modulated and how different light wavelengths, intensities and exposure durations impact the accumulation of GAs in the long term.

Various industrial and domestic processing techniques have been shown to significantly affect the GA content in the potato by either reducing or in some cases even increasing these compounds (Rytel et al. 2015; Elżbieta 2012). Understanding the impact of processing on GA accumulation is critical to ensuring food safety in potato products. Table 1 provides a comprehensive overview of the reduction in GA content by different processing methods, including peeling, thermal processing (frying, boiling, steaming), blanching and new methods (high-pressure processing (HPP), microwave, fermentation). The effectiveness of each method is influenced by factors such as temperature, duration and application method.

Peeling and Surface Removal

Extensive studies have shown that GAs are mainly concentrated in the skin and the outermost 1.5- to 3.0-mm thick layer of potato tubers (Pęksa et al. 2002; Maga 1994; Friedman and Dao 1992). The GA concentration in the peel has been reported to be three to ten times higher than in the inner flesh, making peeling an effective method to reduce GA intake (Lachman et al. 2013). However, the effectiveness of peeling in removing GA varies widely and depends on factors such as the potato genotype, the original glycoalkaloid content and the peeling method. Studies have found a wide range of GA concentrations in potato skins, ranging from 30 to over 1000 mg/kg, while levels in peeled potato can drop to as low as 1.0 mg/kg or remain as high as 45.0 mg/kg (Mondy and Gosselin 1988; Bushway 1983). This variability suggests that peeling efficiency is highly dependent on the initial GA concentration of the tuber. Some studies suggest that the GA content can be reduced by about 50% by peeling, although this reduction varies depending on the potato variety (Nie et al. 2018; Ostrý et al. 2010). Further studies have shown that between 60–96% of GAs can be removed by peeling (Maga 1994). However, for tubers with exceptionally high GA concentrations, peeling alone can only reduce the content by 35%, leading to critical food safety concerns. These results suggest that peeling, while a useful mitigation strategy, may not be sufficient when GA levels exceed safe consumption limits. The effectiveness

Table 1 Effects of different processing methods on the glycoalkaloid (GA) content in potato

Processing method	Effect on GA content	Details	References
Peeling	Reduction by ~ 50%	Effectiveness varies depending on variety and initial GA content. Peeling depth plays a role, with mechanised peeling being more consistent than the manual	Nie et al. (2018), Lachman et al. (2013), Nema et al. (2008), Rytel (2012), Mondy and Gosselin (1988), Bushway (1983)
Frying	Reduction by up to 92%	High-temperature frying (> 160 °C) break down GA via thermal decomposition, with some leaching into oil	Martínez-García et al. (2024), Nie et al. (2018), Tajner-Czopek et al. (2014), Rytel et al. (2005)
Boiling (peeled potato)	Reduction by 15–25%	Reduction occurs through leaching into cooking water, but is limited in unpeeled potato due to glycoalkaloid water insolubility	Wang et al. (2024), Nie et al. (2018), Mondy and Chandra (1979)
Steaming	Limited reduction	No direct contact with water, reducing leaching. This method is less effective than boiling	Wang et al. (2024), Pęksa et al. (2006)
Blanching	Reduction by up to 28%	Blanching at 70–90 °C inactivates enzymes and facilitates leaching. Higher temperatures (85–90 °C) improve GA degradation. Optimum blanching time is 4–5 min	Saini et al. (2023), Liu and Scanlo (2007), Kita et al. (2022), Zhang et al. (2018), Rytel (2012)
High-pressure processing (HPP)	Reduction by breaking up structures without using high temperatures	HPP preserves nutritional and sensory properties while reducing toxicity. Promising for food industry applications	Tsikrika et al. (2021)
Microwaving	Slight reduction	Microwaving for 5–7 min shows a limited reduction. This method is less effective compared to traditional methods such as frying and blanching	Guruprasad et al. (2024), Li et al. (2021)
Fermentation	Potential for reduction	Certain lactic acid bacteria strains can metabolise GA, showing promises to reduce toxicity. Research is ongoing	Afaka et al. (2024), Gong et al. (2024), Li et al. (2021)

GA, glycoalkaloid

of peeling is also influenced by the depth of removal, as glycoalkaloids are often found just below the surface (Lachman et al. 2013; Nema et al. 2008). Industrial processing techniques, such as mechanical peeling, have been shown to be more effective than manual peeling as they consistently remove the surface layers (Rytel 2012). However, excessive peeling can lead to the loss of important nutrients, especially vitamins and dietary fibre, which are concentrated in the outer layers of the tuber (Ostrý et al. 2010). To optimise GA reduction while preserving nutritional value, future research should focus on developing advanced peeling techniques that balance food safety and nutrient preservation. Strategies such as controlled deep peeling, enzymatic treatments or selective breeding of varieties with low GA content could offer promising solutions to reduce the GA load while maintaining the nutritional integrity of potato (Skrabule et al. 2013).

Blanching

Blanching is a widely used pre-treatment for potato, especially before freezing or drying, and plays a crucial role in reducing the GA content. In this thermal treatment, the potato is usually immersed in hot water or steam for a short time and then cooled quickly. Blanching serves to inactivate the enzymes responsible for GA biosynthesis and facilitates the leaching of these compounds from the potato tissue (Saini et al. 2023). Research has shown that blanching temperatures of 70–90 °C are particularly effective in reducing GA content, with higher temperatures such as 85 and 90 °C causing greater inactivation of the enzymes and thus promoting the leaching of GAs (Liu and Scanlon 2007). These higher temperatures also help to reduce reducing sugars, which are important triggers of the Maillard reaction, a crucial process for the development of flavour and colour during cooking. As a result, blanching not only reduces the GA content but also improves the sensory properties of potato products, including colour, crispness, flavour and aroma (Kita et al. 2022). The optimal blanching conditions identified in the literature indicate that a temperature of 85 °C for 4 min provides the best balance between GA reduction and sensory quality. This process effectively reduces the GA content while improving the colour, flavour and crispness of potato products (Zhang et al. 2018). However, too long blanching times or too high temperatures can lead to the degradation of other important nutrients. Therefore, it is important to optimise blanching conditions to maximise GA degradation while maintaining the nutrient integrity of the potato. Blanching has been shown to reduce GA content by up to 28%, with heat-induced degradation and leaching being the most important mechanisms (Rytel 2012). The duration of blanching also plays a decisive role in reducing the GA content. A blanching time of 5–10 min generally leads to a greater reduction in the GA content than a shorter exposure time. Therefore, blanching should be considered as an additional pre-treatment, especially when it comes to ensuring food safety and preserving the nutritional quality of processed potato products (Saini et al. 2023; Liu et al. 2015). Future research should focus on refining blanching protocols to optimise

this balance and ensure both effective reduction of GA content and preservation of important nutrients in processed potato products.

Effects of Thermal Processing

Deep-frying is recognised as an effective thermal processing method for reducing the GA content in potato. Frying at high temperatures, usually above 160 °C, can degrade up to 92% of GAs through thermal decomposition and structural changes in the potato matrix (Nie et al. 2018). The degradation of GAs occurs primarily through thermal decomposition, where high heat breaks down the GA structure, leading to the degradation of α-solanine and α-chaconine to less toxic by-products (Martínez-García et al. 2025; Rytel et al. 2005). In addition, some GAs can pass into the frying oil, further reducing their concentration in the final product. While frying has been shown to be highly effective in reducing GAs, it also raises significant concerns regarding the formation of acrylamide. Therefore, future studies need to carefully evaluate frying conditions to find a balance that optimises GA reduction while minimising the potential for acrylamide formation. In contrast to frying, boiling and steaming have a limited effect on glycoalkaloid degradation. Studies show that boiling peeled potato leads to a modest 15–25% reduction in GA content (Wang et al. 2024). This reduction is primarily due to leaching into the cooking water rather than thermal degradation. However, boiling unpeeled potato has a negligible effect, as GAs are insoluble in water and remain trapped in the potato skin. Steaming is even less effective as there is no direct contact with water, which reduces the potential for leaching (Mondy and Chandra 1979). The limited degradation observed with boiling and steaming suggests that these methods should be combined with other treatments, such as peeling or blanching, to achieve a significant reduction in toxins.

Alternative and Emerging Processing Methods

While conventional processing methods such as peeling and frying have been extensively studied to reduce the GA content in foods, new technologies offer exciting opportunities to reduce GA toxicity more efficiently. Some alternative and innovative methods currently being explored include high-pressure processing (HPP), microwaving and fermentation (Afaka et al. 2024; Guruprasad et al. 2024). Preliminary studies have shown that HPP can effectively break down GA structures and thereby reduce their toxicity. A key advantage of HPP is that this reduction can be achieved without high temperatures, making it a promising technique to preserve the sensory and nutritional properties of food (Tsikrika et al. 2021). This method has potential for applications in the food industry where minimal thermal processing is desired. Although microwave is a widely used cooking technique, its effectiveness in reducing GA content is less pronounced compared to methods such as frying or blanching. Limited research suggests that microwaving food for 5–7 min can lead to a slight reduction in GA content, but this method does not achieve the same level of effectiveness as more traditional approaches (Kondamudi et al. 2017). Further research is needed to optimise this method to reduce GAs. Fermentation, especially when supported by specific strains of lactic acid bacteria, has shown promise for

the degradation of GAs. Although this method is still in the research phase, some studies suggest that fermentation could be a viable option for reducing GA toxicity in food (Afaka et al. 2024; Gong et al. 2024; Li et al. 2021). The ability of certain bacteria to metabolise GAs opens up new possibilities to naturally reduce their levels in food. Although these new methods offer potential benefits, further studies are needed to assess their feasibility and scalability in large-scale food production. As research progresses, these techniques could play an important role in the development of safer and more nutritious foods.

Extraction Methods of Glycoalkaloids

The extraction of GAs from plant materials is crucial for analysing and quantifying these bioactive compounds, which are important in various fields such as food safety and pharmacology (Patel et al. 2021; Ruprich et al.2009). Extraction methods for GAs vary in terms of their efficiency, cost, environmental impact and applicability to different matrices. Several extraction techniques have been developed, each with their own modifications, advantages, and limitations (Table 2). Understanding these factors is crucial for selecting the most appropriate method, depending on research objectives and available resources. A common approach for GA extraction is the methanol–water method (Maldonado et al. 2014), which often includes solid-phase extraction (SPE) and column purification steps. The use of SPE increases the purity of the extracted GAs by selectively retaining certain compounds, thereby improving the quality of the extract. Column purification further refines the extract and isolates the GAs from unwanted substances (Perez and Albero 2023). Acetic acid, a widely used solvent, is often added to improve the efficiency of extraction. This method is praised for its high recovery rates and relatively simple preparation process, making it a popular choice for many studies (Bejarano et al. 2000). However, the need for additional purification steps after extraction can complicate the process and make it more time and labour intensive (Musita et al. 2020; Tajner-Czopek et al. 2014; Wang et al. 1972).

Modifications such as butanol partitioning, SPE coupled with HPLC (SPE-HPLC) and the addition of sodium bisulphite can significantly improve the efficiency and specificity of the extraction (Machado et al.2007). Butanol partitioning is particularly useful for complex matrices as it separates compounds based on their polarity (Topolwska and Haliński 2024; Aziz et al. 2012). Additional SPE followed by HPLC offers high sensitivity and precision, making it ideal for applications requiring detailed analysis and quantification (Perez and Albero 2023). In addition, the use of sodium bisulphite in combination with C18 SPE improves selectivity for GAs, but can also lead to degradation of the target compounds, limiting the stability of the extract (Machado et al. 2007). Although butanol separation is effective for the extraction of GAs from potato peels and flesh, the separation process is laborious and can increase the overall time for analysis (Topolwska and Haliński 2024; Valcárcel et al. 2014; Aziz et al. 2012; Machado et al. 2007; Sotelo and Serrano 2000).

Extraction with organic solvents such as methanol–chloroform, water–ethanol and heptanesulfonic acid in combination with SPE is also used to extract GAs (Friedman et al. 1997). The methanol–chloroform combination is very effective for dry

Table 2 Comparison of glycoalkaloid extraction methods in potato

Extraction method	Key additional step	Advantages	Disadvantages	Reference
Methanol–water	+ SPE	High recovery, simple preparation	Requires further purification	Musita et al. (2020), Maldonado et al. (2014)
	+ Column purification	Improved specificity	Time-consuming, labour-intensive	Tajner-Czopek et al. (2014)
	+ Acetic acid	Cost-effective, widely used	May co-extract impurities	Bejarano et al. (2020)
Acetic acid-based	+ Butanol partitioning	Effective for complex matrices	Requires additional steps	Sotelo and Serrano (2000)
	+ SPE + HPLC	High sensitivity and precision	Expensive, requires expertise	Machado et al. (2007), Knuthsen et al. (2009)
	+ Sodium bisulphite + C18 SPE	Good selectivity for GAs	Risk of degradation	Valcárcel et al. (2014)
	+ Butanol partitioning	Suitable for peels and flesh	Laborious separation process	Aziz et al. (2012)
	+ Butanol + GC	Highly accurate quantification	Requires specialised equipment	Topolwska et al. (2024)
Organic solvent-based	+ Methanol-chloroform	Efficient for dry samples	Toxic solvents, hazardous waste	Friedman et al. (1997)
	+ Water–ethanol	Safe, eco-friendly	Less efficient for non-polar compounds	Maldonado et al. (2014)
	+ Heptanesulfonic acid + SPE	Improved selectivity	Requires specific reagents	Abreu et al. (2007)
Ultrasound-assisted extraction (UAE)	Applied to *Solanum* vs. *Chacha* varieties	Fast, efficient, minimal solvent use	Equipment-intensive	Martínez-García et al. (2024)
Tetrahydrofuran-water-acetonitrile	+ LC detection	High sensitivity	Expensive, not widely used	Bushway et al. (1979)

SPE, solid-phase extraction; *HPLC,* high-performance liquid chromatography; *LC,* liquid chromatography; *GAs,* glycoalkaloids

samples, especially those rich in non-polar compounds. However, the use of chloroform, a toxic solvent, raises safety and environmental concerns, making this method less desirable in environments with strict safety regulations or where environmentally friendly procedures are required. On the other hand, extraction with water–ethanol is safer and more environmentally friendly, offering a non-toxic alternative to chloroform. While this method is relatively safe, it may not be as efficient at extracting non-polar GAs, which could limit its applicability in certain contexts. Heptanesulfonic acid in combination with SPE improves selectivity for GAs, but requires specialised reagents that are not available in all laboratories. Despite these limitations, extractions with organic solvents provide reliable methods for GA isolation, especially when analysing dry plant material (Maldonado et al. 2014; Abreu et al. 2007; Friedman et al. 2003). Ultrasound-assisted extraction (UAE) has gained popularity due to its speed and efficiency (Demesa et al. 2024; Shen et al. 2023). In this technique, ultrasonic waves are used to enhance the extraction process, resulting in faster extraction times and lower solvent consumption. The UAE method is particularly effective in the extraction of GAs from *Solanum* species, as demonstrated in several studies (Martínez-García et al. 2024; Hossain et al. 2015; Li et al 2009). The fast extraction process and low solvent requirements make it an attractive option for high-throughput analyses. However, the need for specialised equipment such as ultrasonic baths or probes makes UAE method very costly. This can be a limiting factor for laboratories that do not have access to such technologies, especially in resource-limited areas (Martínez-García et al. 2024). Tetrahydrofuran–water–acetonitrile extraction combined with liquid chromatography (LC) detection offers high sensitivity and precision in the quantification of glycoalkaloids. The combination of these solvents provides a robust method for the extraction of GAs, and the use of LC ensures accurate and reliable quantification of the compounds. However, this method is expensive and not widely used as it requires sophisticated instrumentation and trained personnel. The high costs associated with LC detection make it less accessible to many research laboratories and limit its use in routine analyses (Bushway et al. 1979).

To summarise, the extraction of GAs involves a variety of methods, each with its own advantages and limitations. Methanol–water extraction combined with solid-phase extraction (SPE) offers simplicity and high recoveries, although it may require additional purification steps to remove co-extractives. While methanol is inherently toxic, its use in this context is strictly confined to laboratory-based analytical procedures. All extractions are performed under controlled conditions, and the solvent is fully removed prior to quantification. Acetic acid-based methods offer high sensitivity and precision, but are costly and labour-intensive. Organic solvent-based methods such as methanol–chloroform are effective but raise safety and environmental concerns due to toxicity and volatility. In contrast, ethanol–water mixtures are widely considered food-safe and are preferred for applications involving edible products, although their large-scale use may still require attention to solvent recovery and flammability. UAE is efficient and environmentally friendly but requires specialised equipment. Finally, tetrahydrofuran–water–acetonitrile extraction with LC detection offers high sensitivity but is expensive and requires access to modern equipment. The choice of method depends on the specific research requirements, the available resources and the complexity of the sample matrix.

Analytical Methods for Glycoalkaloid Detection and Quantification

The accurate quantification of GAs is crucial for food safety, breeding programmes, and quality control in the food industry. Various analytical methods have been developed for the determination of GAs, each with different principles, advantages and limitations (Table 3). The quantification of GAs has historically relied on HPLC, which continues to be a cornerstone technique in analytical and quality control laboratories. HPLC enables the separation and quantification of major GAs—particularly α-solanine and α-chaconine—from complex matrices such as potato tuber extracts, based on differences in polarity and retention behaviour (Valcárcel et al., 2014; Kasnak & Artik 2018). When coupled with detectors such as ultraviolet (UV), diode array (DAD) or fluorescence, the method provides reliable and reproducible quantification, making it suitable for large-scale surveys and regulatory monitoring (Sotelo and Serrano 2000; Aziz et al. 2012; Knuthsen et al. 2009). HPLC has been successfully applied to a wide range of potato genotypes, including local and commercial varieties, confirming its utility in breeding programs and cultivar selection aimed at minimizing GA content (Martínez-García et al. 2024; Musita et al. 2020; Amer et al. 2014). Its relatively high throughput and established protocols make it ideal for routine use, especially when target compounds are well characterised.

However, the technique is not without limitations. The sensitivity of UV-based detection can be insufficient for trace-level analysis, and co-elution of matrix constituents may compromise quantification accuracy. Moreover, HPLC lacks the ability to resolve structurally similar isomers or to identify unknown GA analogues, thus limiting its application in untargeted profiling and discovery-driven research (Bejarano et al., 2020). The method also requires time-intensive sample preparation, skilled operators and access to well-maintained instrumentation, which can constrain its use in resource-limited settings (Şengül et al. 2004; Abreu et al. 2007). These limitations have prompted the increasing adoption of mass spectrometry-based methods, particularly LC–MS/MS, which offer enhanced sensitivity, selectivity and structural resolution for GA profiling.

LC–MS/MS has emerged as a gold-standard technique for the sensitive, specific and structurally informative quantification of GAs in plant-based matrices (Urban et al. 2018). By integrating the high-resolution separation of liquid chromatography with the molecular selectivity of mass spectrometry, LC–MS/MS enables the accurate detection of trace levels of GAs, including poorly characterised or novel analogues (Popova et al. 2022). Its ability to resolve isomeric structures and elucidate fragmentation patterns provides crucial insights into the chemical diversity and biosynthetic complexity of steroidal alkaloids, particularly in non-model matrices such as potato protein isolates (Deußer et al. 2012). Among the various acquisition modes, selected ion monitoring (SIM) has demonstrated particular utility in enhancing quantification performance. Unlike full-scan approaches that record a wide m/z range and often suffer from reduced sensitivity, SIM focuses on a predefined set of ions, allowing for more data points per analyte and thus increasing sensitivity by an order of magnitude. This was clearly demonstrated by Nielsen et al. (2020), who reported a ~ tenfold improvement in signal intensity when quantifying

Table 3 Comparison of different analytical techniques for the quantification of glycoalkaloids in potato

Technique	Principle	Advantage	Disadvantage	Column/Instrument	Varieties (Country)	Extraction method	Total glycoalkaloids	References
HPLC	Separation based on polarity	Highly accurate and precise for separating and quantifying individual glycoalkaloids Allows analysis of complex matrices with minimal interference Widely used, well-established and allows high throughput analysis Can be coupled with detectors (UV or fluorescence) for increased sensitivity	Requires expensive equipment and consumables Sample preparation is time-consuming and needs specialised skills Lower sensitivity than advanced techniques such as LC–MS/MS Not ideal for detecting unknown or complex glycoalkaloids without prior knowledge	EC-C18 column (2.7 µm, 3.0 mm i.d. × 150 mm)	Agata, Agria, Amandine, Amaris, Caesar, Colomba, Evolution, Frisia, Lady Amarilla, Memphis, Monalisa, Rudolph, Soprano, Universa, Vivald (Spain)	Solvent extraction and ultrasound-assisted extraction (UAE) using sonication (75% amplitude)	α-Solanine 143.0–1273.0 mg/kg DW; α-chaconine 117.0–1742.0 mg/kg DW	Martínez-García et al. (2024)
				Mikrosorb NH_2 (25 × 46 cm L.D.)	Herbie 26, High-land Burgundy Red (red-fleshed); Blue Congo, Vitelotte (blue-fleshed) (Czech Republic)	Freeze-dried material extracted with water and methanol, purified with special column, dissolved and filtered	Unpeeled potato 40.8–60.9 mg/kg FW; peeled potato 18.1–31.3 mg/kg FW	Tajner-Czopek et al. (2014)

Table 3 (continued)

Technique	Principle	Advantage	Disadvantage	Column/Instrument	Varieties (Country)	Extraction method	Total glycoalkaloids	References
				Zorbax C18 (5 µm, 4.6×150 mm)	Unknown varieties (Ireland)	1 g peel or 7 g flesh freeze-dried tissue using water-acetic acid-sodium hydrogen sulphite solution, then purified with C18 SPE column	Flesh: 4.0–957.0 mg/kg DW; peel: 150.0–8133.0 mg/kg DW	Valcarcel et al. (2014)
				Nucleosil NH_2 (5 µm, 4.0×250 mm)	May Queen (USA)	Chloroform and methanol extraction, dissolved in HCl, precipitated and redissolved in acetonitrile	Wet flesh: 1.0 mg/kg; dry peel: 2581.0 mg/kg	Friedman and Dao (1992)
				C18 (5 µm, 250×4.6 mm i.d.)	Raja and Santé (Portugal)	50 g of the tubers extracted with heptane sulfonic acid sodium salt and purified with solid-phase extraction (SPE)	Santé: 81.5 mg/kg FW; Raja: 79.5 mg/kg FW	Abreu et al. (2007)
					Potosina, Chapaquita, Pampena (drought-tolerant improved hybrids), Malcacho, Sani Imilla (Belgium)	2.5 g tubers homogenised with water-acetic acid-sodium bisulphite, centrifuged, passed through SPE	Drought-resistant: 29.0–100.0 mg/kg FW; commercial: 34.1–122.3 mg/kg FW	Bejarano et al. (2020)

Table 3 (continued)

Technique	Principle	Advantage	Disadvantage	Column/Instrument	Varieties (Country)	Extraction method	Total glycoalkaloids	References
					Shangi, Dutch Robijn, Royal (Kenya)	Homogenising freeze-dried samples with methanol and water, followed by filtration and solid-phase extraction	104.8–515.6 mg/kg DW	Musita et al. (2020)
					Monalisa (Brazil)	0.5 g freeze-dried samples mixed with 10 mL of extraction solution (water, acetic acid, sodium bisulphite), shaken for 15 min and centrifuged at 4000 rpm/20 min	51.4–107.9 mg/kg FW	Machado et al. (2007)
					Atlantic (white-flesh), Purple Majesty (purple-flesh), Yukon Gold (yellow-flesh), advanced selection (CO97227-2P/PW) (USA)	5 g potato chips extracted with acetone, chloroform and aqueous acetone, stored at − 20 °C	93.1–105.1 mg/kg FW	Amer et al. (2014)

Table 3 (continued)

Technique	Principle	Advantage	Disadvantage	Column/Instrument	Varieties (Country)	Extraction method	Total glycoalkaloids	References
					Diamant, Cardinal (Pakistan)	500 mg peel and 1500 mg flesh extracted with 5% acetic acid, partitioned with butanol, dried and dissolved in methanol	Peel: 1772–54,499 mg/kg DW; flesh: 31.0–147.0 mg/kg DW	Aziz et al. (2012)
				C18 Atlantis column (5 µm, 3.9 mm × 150 mm; Waters Corp.)	Agria, Bettina (Turkey)	10 g sample were homogenised in 40 mL extraction solution (water-acetic acid-sodium hydrogen sulphide) for 15 min in Ultra-Turrax T-50 homogeniser	Bettina: 234.3 mg/kg DW	Kasnak and Artik (2018)
					Folva, Sava, Bintje, Ditta, Asparges, Marabel, Annabelle, Solist, Nicola, Ostara, Charlotte, Berber, Maris Peer, Asparges, Arielle, Solara, Revelino, Lady Christel, Sieglinde, Lammefjord, Vildmose (Denmark)	Dry samples were homogenised and stored at − 20 °C before extraction with solution of water, acetic acid and sodium hydrogen sulphite. Extracts were cleaned using SPE columns and eluted with a mobile phase, then adjusted to 5 mL	9.0–280.0 mg/kg DW	Knuthsen et al. (2009)

Table 3 (continued)

Technique	Principle	Advantage	Disadvantage	Column/Instrument	Varieties (Country)	Extraction method	Total glycoalkaloids	References
				µBonda-Pak C18 (3.9 × 300 mm)	Alpha, Atzimba, Juanita, López, Marciana, Michoacán, Montsama, Murca, Nortenã, Puebla Rosita, Tollocan (Mexico)	Acetic acid extraction + Butanol partitioning	Peel: 29.0–916.3 mg/kg FW; flesh: 6.3–83.7 mg/kg FW	Sotelo and Serrano (2000)
				Pbondapak NH_2 (30 cm × 4 mm L.D.)	Unknown variety (USA)	Samples extracted with tetrahydrofuran-water-acetonitrile	α-Solanine 16.2 ± 1.7 mg/g DW; α-chaconine 28.4 ± 3.3 mg/g DW	Bushway et al. (1979)

Table 3 (continued)

Technique	Principle	Advantage	Disadvantage	Column/Instrument	Varieties (Country)	Extraction method	Total glycoalkaloids	References
LC–MS/MS	Ionisation and mass fragmentation	High sensitivity and specificity for trace-level glycoalkaloid quantification Detects wide range of glycoalkaloids including isomers, with greater specificity than HPLC Enables structural identification and confirmation Ideal for complex samples, offering detailed profiles	High equipment and maintenance costs, limiting accessibility Requires specialised training for operation and result interpretation Time-consuming with complex sample preparation (e.g. derivatisation) Not suitable for routine, large-scale analysis due to process complexity	Dionex Ultimate 3000 HPLC system coupled with an API3200 tandem MS	SYN-PLANTS, Vitelotte, Bintje (Luxembourg)	150 mg freeze-dried potato powder extracted with methanol–water-acetic acid, vortexed, centrifuged, evaporated and resuspended	Peel: 585–5342 mg/kg DW; flesh: 7.0–466.0 mg/kg DW	Deußer et al. (2012)
				UHPLC-MS/MS system consisted of a Dionex UltiMate 3000 RSLCnano system	Unica, Lishu (Chine)	Extraction of samples with a 10% acetic acid aqueous solution	Recovery: 86.3–92.3% (flesh); 86.5–90.5% (peel)	Nie and Guo (2017)

Table 3 (continued)

Technique	Principle	Advantage	Disadvantage	Column/Instrument	Varieties (Country)	Extraction method	Total glycoalkaloids	References
				LC–MS/MS	Unknown variety (Poland)	4 g freeze-dried potato extracted with 5% aqueous acetic acid, purified with butanol-water, evaporated and reconstituted in methanol	21.2 ± 1.4 mg/kg DW	Topolwska et al. (2024)
				UFLC-MS system, Kinetex PFP column (2.6 µm, 100 × 3.0 mm)	Russet (Canada)	Peels extracted with acidified water–ethanol, stirred, sonicated and centrifuged	α-Solanine 71.0 mg/kg FW; α-chaconine 170.0 mg/kg FW	Maldonado et al. (2014)
				HPLC-ESI/MS/MS, Pinnacle DB C18 (1.9 µm, 50 × 2.1 mm)	Agria (yellow-fleshed), Russet Burbank (white-fleshed), purple-fleshed varieties, red-fleshed varieties (Czech Republic)	Fresh, freeze-dried and processed potato homogenised and extracted with acetic acid, butanol-partitioned	33.7–167.8 mg/kg FW	Urban et al. (2018)

Table 3 (continued)

Technique	Principle	Advantage	Disadvantage	Column/Instrument	Varieties (Country)	Extraction method	Total glycoalkaloids	References
ELISA	Antibody-based detection	Fast, cost-effective and ideal for large-scale screening Minimal sample preparation, highly specific for targeted glycoalkaloids Provides fast results with high throughput for routine monitoring Can be automated for efficient industrial or agricultural testing	Limited sensitivity, not ideal for trace analysis Requires specific antibodies, which may not be available for all compounds Risk of cross-reactivity or false positives with non-specific antibodies Not suitable for profiling multiple glycoalkaloids	ELISA Kit/the wavelength of the ELISA plate reader was set at 450 nm	Russet, organic Russet, Yukon Gold, Small Purple, Small Red, Small Gold, Large White, Small White (USA)	Various samples extracted with 2% acetic acid, partitioned with butanol	1.2–41.0 mg/kg FW	Friedman et al. (1998)
				HRP labelling kit—SH/wavelength of 490 nm by a microplate reader	Irish Cobbler (Japan)	Potato components (sprouts, peels, tubers) were homogenised in 10% DMSO, centrifuged and supernatants were collected for assay samples	Tuber: 22.0–63.28 mg/kg FW; peel: 327.1–510.2 mg/kg FW; sprout: 1892–5423 mg/kg FW	Okada and Matsuo (2023)

Table 3 (continued)

Technique	Principle	Advantage	Disadvantage	Column/Instrument	Varieties (Country)	Extraction method	Total glycoalkaloids	References
Colorimetric	Colorimetric reaction with DMAB	Ideal for total glycoalkaloid content and quality control Accessible without expensive equipment	Less sensitive Only measures total glycoalkaloid content, not individual compounds or isomers Requires longer processing time and may have higher variability Not suitable for complex matrices with diverse glycoalkaloids	Wavelength 600 nm using a spectrophotometer	Lord, Irga, Vineta, Bellarosa (Poland)	10 g grated tuber mass was methanol-extracted for 10 min, filtered and made up to 50 cm^3, 5 cm^3 was evaporated and analysed at 620 nm	34.9–89.7 mg/kg FW	Rymuza et al. (2020)

Table 3 (continued)

Technique	Principle	Advantage	Disadvantage	Column/Instrument	Varieties (Country)	Extraction method	Total glycoalkaloids	References
				Wavelength 565–570 nm using a spectrophotometer	Draga, Sponta (Jordan)	20 g potato fresh samples were macerated in acidified ethanol, filtered and heated at 70 °C/30 min. Glycoalkaloids were precipitated by adjusting pH to 10 with ammonium hydroxide, centrifuged, washed, dried and quantified	Skin: 258–1280 mg/kg FW	Haddadin et al. (2001)
				Wavelength 600 nm using a spectrophotometer	Fresh potato and industrial potato protein (Netherlands)	Potato samples were refluxed in ethanol (80% or 96%) at 90 °C/15 min, concentrated, acidified (10% acetic acid), centrifuged, alkalised (pH 10), heated (70 °C/20 min), cooled (4 °C/3 h), recentrifuged and glycoalkaloid pellet was dissolved in 7% phosphoric acid	50–1650 mg/kg DW	Bergers (1980)

DW, dry weight; *FW*, fresh weight

α-solanine, α-chaconine and solanidine in protein-rich potato samples. The study also highlighted a key methodological limitation: co-elution with matrix constituents impaired chromatographic resolution, leading to potential overestimation in GA quantification due to peak area inflation. Nevertheless, the method enabled tentative identification of minor GA analogues, including β-solanine (m/z 706/722), γ-solanine (m/z 560), β-chaconine (m/z 706) and γ-chaconine (m/z 560), emphasizing its potential for semi-targeted profiling within complex food matrices. Despite its analytical power, LC–MS/MS presents notable limitations. The instrumentation is capital-intensive, requires regular maintenance and demands skilled personnel for method development, operation and data interpretation. Moreover, extensive sample preparation and relatively low throughput restrict its scalability for routine screening in industrial or agricultural contexts (Donno et al. 2020). These constraints notwithstanding, LC–MS/MS remains indispensable in research-driven investigations that demand high analytical depth, structural resolution and the discovery of novel or minor GA analogues. However, given the structural diversity of GAs – including both polar, glycosylated forms and non-polar aglycones – gas chromatography–mass spectrometry (GC–MS) has also proven valuable, particularly for the analysis of volatile, thermally stable, or derivatised compounds. GC–MS has played a pivotal role in the structural elucidation of aglycone backbones, such as solanidine, solasodine and related alkaloid fragments, often following hydrolysis or chemical derivatisation (Alt et al. 2005). Although less suited for intact GA profiling due to thermal instability and polarity, GC–MS remains a complementary tool for untargeted metabolomics and the characterisation of breakdown products. Together, LC–MS/MS and GC–MS constitute the analytical foundation for GA research, enabling both targeted quantification and in-depth structural characterisation across diverse matrices and compound classes (Topolewska and Haliński 2024). The enzyme-linked immunosorbent assay (ELISA) is a widely used immunological method for the detection and quantification of GA in potato samples. This technique is based on the use of GA-specific antibodies that bind to the target substances and cause a measurable colour change (Driedger et al. 2000). ELISA offers a fast and cost-effective solution for large-scale screening, especially in quality control and industrial applications. It has already been used to monitor GA levels in raw materials and processed potato (Friedman et al. 1998). ELISA is known for its speed and cost-effectiveness, making it an excellent choice for high-throughput analyses. The method is relatively easy to perform, requires minimal sample preparation and provides rapid results. In addition, it can be customised for automated systems, further increasing its efficiency for large-scale screening (Okada and Matsuo 2023). ELISA is also well suited for routine monitoring, especially in situations where multiple samples need to be tested quickly and cost-effectively. Although ELISA offers numerous advantages, it also has its limitations. The main disadvantage is its lower sensitivity compared to more advanced techniques such as LC–MS/MS and HPLC. ELISA is also limited in its ability to differentiate between specific GA compounds, as it usually only detects a subset of the GAs for which the antibody is specific (Morgan et al. 1983). In addition, the possibility of cross-reactivity between antibodies and other compounds in the sample can lead to false positive results, making interpretation of the results difficult.

The Bergers colourimetric method is a classical and straightforward approach for the quantification of total GAs in potato (Bergers 1980). This technique involves a colourimetric reaction with the 4-dimethylaminobenzaldehyde (DMAB), which causes a colour change that correlates with the concentration of GAs. It has been used for decades as a rapid, cost-effective method for preliminary or routine screening of GA content in potato (Rymuza et al. 2020; Sreevidya and Mehrotra 2003; Haddadin et al. 2001). The main advantage of the Bergers method is its simplicity and cost-effectiveness. It requires only minimal equipment, making it applicable even in resource-poor areas. The technique is also fast and delivers results in a short time. Due to its ease of use, the Bergers method is often used in quality control and preliminary investigations where accurate quantification is not required. Despite its simplicity, the Bergers method has some significant disadvantages. Its sensitivity is relatively low compared to more sophisticated techniques such as LC–MS/MS and HPLC. In addition, the method only provides a measure of the total GA content without distinguishing between different GA compounds or their isomers. It is therefore not suitable for the detailed analysis of specific GA. The accuracy of the method can also be affected by interference from other compounds in the sample matrix (Coxon et al. 1979).

When selecting the most appropriate analytical method for the quantification of GAs, researchers must carefully consider several key factors, including the complexity of the sample, the sensitivity required and the resources available. Each method has certain advantages depending on the analytical objectives and limitations. HPLC is an established technique commonly used for the precise quantification of known GAs, particularly in routine laboratory analysis. It is effective for the quantification of major GAs such as α-solanine and α-chaconine. However, its sensitivity may be insufficient for the detection of trace concentrations or for the structural analysis of more complex GAs. On the other hand, LC–MS/MS offers unrivalled sensitivity and specificity, making it the gold standard for comprehensive GA profiling. This method is characterised by the detection of low concentrations and provides detailed structural information that is valuable for in-depth studies of GA composition. However, the high cost of the equipment and the need for specialised expertise limit the accessibility of this method, especially for routine applications or in resource-limited environments. For high-throughput screening, especially in industry or agriculture, ELISA offers a practical and cost-effective solution. This immunological method is particularly suitable for large-scale monitoring of GA levels. Although it is fast and inexpensive, it is not as sensitive and specific as required for detailed quantification or structural analysis of GAs, making it less suitable for more sophisticated studies. Finally, the Bergers colourimetric method remains a simple and affordable option, especially in resource-constrained environments. It is typically used for basic screening and provides a quick measure of total GA content (Bergers 1980). However, due to its low sensitivity, inability to distinguish between specific GA compounds, and lack of precision, it is not suitable for detailed or accurate quantification. Ultimately, the choice of an analytical method should be determined by the specific objectives of the analysis—whether it is routine monitoring, detailed profiling or large-scale screening. Available resources, sensitivity requirements and the complexity of the sample matrix must also be considered. In many cases, a combination of these

methods can provide the most comprehensive and reliable results, balancing accuracy, cost and throughput to meet the requirements of different analysis scenarios (Shabir et al. 2007).

Evolving Challenges in Glycoalkaloid Analysis: A Historical and Methodological Perspective

Over the last five decades, research on GAs has seen a significant increase in publications. In the 1960s, the main focus was on their chemical properties and toxicity. In the decades that followed, particularly in the 1980s and 1990s, the scope expanded to include studies on biosynthetic pathways, health concerns and improved analytical techniques for detection (Friedman et al. 1997). Since the 2000s, research has expanded further to include applications in food safety, bio-purposing and the development of methods to reduce GA concentrations in food. This development underlines the increasing recognition of the dual importance of GAs in plant biology and human health and signals a shift towards interdisciplinary approaches aimed at exploiting their benefits while managing the associated risks.

The Era of Basic Quantification (1960s–1990s)

Research on GAs began in the mid-twentieth century, driven by the need to understand their toxic effects in food crops (Osman et al. 1978). Early studies were limited by basic extraction techniques and inadequate analytical methods. Early research on GAs faced significant challenges due to rudimentary analytical techniques, environmental variability and complex extraction methods. In the 1960s and 1970s, researchers such as Berug (1962) and Coxon et al. (1979) relied on basic wet-chemical methods that could only measure total GA content without distinguishing between specific compounds like solanine and chaconine, limiting their ability to assess toxicity accurately (Filadelfi and Zitnak 1983). Environmental factors, including light exposure, further complicated research, as fluctuating GA levels in potato made it difficult to standardise measurements and regulate safe consumption (Berug 1962). Early extraction methods were inefficient, with the presence of lipids in potato extracts necessitating labour-intensive clean-up procedures, which led to low recovery rates and inconsistent results across studies (Rodriguez-Saona et al 1999; Friedman and Dao 1992). The introduction HPLC in the 1970s provided more reliable differentiation of GAs, but challenges like high baselines and poor separation persisted, affecting sensitivity and reproducibility (Friedman and Dao 1992). Inconsistent extraction and analytical methods hindered accurate quantification, making comparisons between studies problematic. Additionally, the lack of specificity in early techniques prevented a detailed understanding of the varying toxicities of different GAs, such as the more significant health risks posed by solanine (Friedman and Dao 1992). As a result, the pharmacological potential of GAs, including their antimicrobial and anticancer properties, remained largely unexplored due to the inability to reliably quantify low levels (Smith et al. 1996). Post-harvest

management and storage conditions, also influencing GA content, were underexplored for many years, adding complexity to managing safe GA levels in crops. Overcoming these challenges required advancements in analytical techniques and agricultural practices, ultimately allowing for a more comprehensive understanding of GA toxicity and pharmacology.

The study of GAs before 2000 reflects both the challenges and significant progress in understanding these compounds. Early studies, limited by rudimentary methods, primarily focused on identifying solanine and understanding its toxic effects. However, advancements in analytical techniques, such as the introduction of HPLC in the 1970s and 1980s, allowed for the separation and quantification of individual GAs, laying the foundation for more detailed research. Despite these advancements, issues such as poor recovery rates and the need for optimised extraction methods remained prominent challenges. By the 1990s, there was a shift in focus towards the potential therapeutic properties of GAs, with researchers recognizing their dual nature as both toxic and potentially beneficial compounds. This evolving understanding underscored the need for precise and accurate measurement methods. Environmental factors were also increasingly recognised as playing a key role in regulating GA levels, adding complexity to the research and highlighting the importance of agricultural practices and post-harvest management.

Technological Advancements and Methodological Refinements (2000s–2010s)

The early 2000s marked a decisive turning point towards more sophisticated analytical techniques. GC–MS became a valuable tool for GA profiling (Alt et al. 2005) and enabled better structural elucidation of aglycones (Arnqvist et al. 2003). However, GC–MS had its own limitations, most notably the inability to analyse intact GAs. The thermal instability of these compounds meant that the high temperatures used in GC–MS could lead to degradation of the glycosidic bonds, resulting in an underestimation of the total GA content. As a result, GC–MS proved to be unsuitable for a comprehensive quantification of GA in potato extracts. At the same time, LC–MS gained importance as an alternative, as it offers higher specificity and the potential for structural elucidation of new GAs (Shakya and Navarre 2008; Väänänen et al. 2005). However, LC–MS also faces major challenges. The lack of commercially available standards for rare GAs and aglycones limited its accuracy, and the method's reliance on fragmentation patterns for identification made it difficult to resolve isomeric overlaps (Cataldi et al. 2005). Research during this period also began to uncover the complexity of GA biosynthesis and metabolism. While earlier studies had focused primarily on α-solanine and α-chaconine, emerging research revealed a broader spectrum of GAs with different toxicological profiles (Mensinga et al. 2005). However, the biosynthetic pathways that regulate the synthesis of GAs remained poorly understood, making it difficult to develop targeted breeding strategies to reduce GA content in potato (Sørensen et al. 2008). The analytical challenges of quantifying these compounds are exacerbated by the increasing complexity of their biosynthesis, which presents a double obstacle to understanding and controlling their presence in crops.

Contemporary Challenges and the Future of Glycoalkaloid Research (2010s–Present)

Despite significant advances in analytical methods, the investigation of GAs is still characterised by persistent challenges in both detection and toxicological assessment. Technological innovations, coupled with growing concerns about food safety and stricter regulatory requirements, have driven the continued refinement of research methodologies (Omayio et al. 2016). Recent studies have focused on the biosynthesis of steroidal GAs, with particular attention to the enzymes and genetic factors involved in their formation (Akiyama et al. 2025; Umemoto et al. 2016). This new knowledge is crucial for understanding how the amount of GAs in potato can be regulated through breeding. At the same time, there is growing interest in the potential therapeutic properties of GAs, including their antimicrobial and anticancer effects (Manoharan et al. 2024; Tang et al. 2023; Winkiel et al. 2022). However, there are still numerous challenges. One of the biggest hurdles in GA analysis is still the difficulty in fully separating these compounds using chromatographic methods. Although HPLC is still the most commonly used technique, it reaches its limits with small sample quantities, as detection limits are typically 100 ppm (Hossain et al. 2015). Furthermore, separation on a preparative scale is still inefficient and often requires optimisation of the method to avoid co-extraction of interfering compounds such as pigments (Bejarano et al. 2020). Despite the high specificity of techniques such as LC–MS, chromatographic separation of GAs remains a critical limiting factor in the analysis process (Popova et al. 2022). Furthermore, the extraction and purification of GAs pose an additional challenge. Conventional solvent-based extraction methods, while effective, are environmentally harmful and can leave solvent residues in the final extracts, leading to sustainability concerns. Alternative environmentally friendly extraction methods, such as supercritical fluid extraction and enzyme-assisted extraction, have been explored but have not yet gained acceptance due to their high cost and limited scalability (López-Lorente et al. 2022). The search for efficient, sustainable extraction methods will be an important area to focus on. The toxicological assessment of GAs remains an active area of research. While acute toxicity is well documented, the long-term effects of chronic exposure and the potential synergistic interactions between GAs and other dietary constituents are not yet fully understood. The metabolism of these compounds in the human gut, particularly with regard to enzymatic hydrolysis and absorption, is still poorly characterised, making risk assessments and regulatory decisions difficult. In addition to these challenges, there is a constant tension between the beneficial and harmful effects of GAs. Their toxicity is a known issue, but their potential therapeutic applications make their investigation even more complex. Further research into GAs must strike a balance between exploiting their bioactive properties and minimising their toxicological risks. From an agricultural perspective, breeding strategies aimed at reducing GA content in potato face a dilemma. GAs play a crucial role in plant defence against pests and pathogens, and efforts to reduce their content could inadvertently make plants more susceptible to disease (Sivasankara Pillai and Dandurand 2021). The challenge for modern plant breeding is to modulate GA biosynthesis in a way that minimises toxicity and maintains plant resistance.

Practical Applications and Implications of Glycoalkaloids

The therapeutic potential of GAs, naturally occurring compounds in Solanaceae plants, has garnered increasing scientific interest due to their multifaceted pharmacological activities (Manoharan et al. 2024; Von Fournier et al. 2024; Popova et al. 2022; Patel et al. 2021; Ni et al. 2018). Among their most documented properties are their anti-inflammatory and analgesic effects, primarily mediated through the inhibition of key pro-inflammatory pathways such as NF-κB and the downregulation of cytokines including IL-6 and TNF-α (Tang et al. 2023; Kenny et al. 2013). This suggests potential applications of GAs in managing chronic inflammatory disorders such as arthritis. Beyond inflammation, GAs also exhibit robust antioxidant capacity, functioning as potent scavengers of reactive oxygen species (ROS), thereby protecting cellular components from oxidative damage (Hasanain et al. 2015). This antioxidative function is of critical importance in the prevention of diseases where oxidative stress plays a pathogenic role, including cardiovascular and neurodegenerative diseases. In addition to these protective roles, GAs have demonstrated promising anti-cancer activities. Studies indicate that compounds such as α-solanine and α-chaconine can induce apoptosis, inhibit cell proliferation and interfere with tumour cell signalling pathways, often with selective cytotoxicity toward cancer cells while sparing normal tissues (Gu et al. 2021; Yan et al. 2020; Lv et al. 2014c; Sun et al. 2014; Lu et al. 2010; Lee et al. 2004). This selectivity underscores their value as potential leads in the development of less toxic chemotherapeutic agents. Moreover, the antimicrobial potential of GAs deserves particular attention in the current context of escalating antibiotic resistance. Several in vitro studies have demonstrated that GAs exhibit broad-spectrum antimicrobial activity, with marked efficacy against Gram-positive bacterial strains (Sołtys-Kalina et al. 2023; Liu et al. 2020; Ismail et al. 2019; Sánchez-Maldonado et al. 2016; Amanpour et al. 2015). Their mechanism of action is thought to involve disruption of bacterial cell membrane integrity, leading to increased permeability and subsequent cellular dysfunction. This positions GAs as promising candidates for the development of novel antimicrobial agents derived from natural products (Sivasankara Pillai and Dandurand 2021). Nonetheless, despite these compelling bioactivities, their pharmacological use is constrained by a limited therapeutic index, as higher concentrations may exert cytotoxic effects on non-target cells. Future research should therefore focus on pharmacodynamic profiling, targeted delivery systems and rigorous clinical validation to fully exploit their therapeutic potential while ensuring safety and efficacy (Patel et al 2021). Recent research by Wolters et al. (2023) has highlighted the promising potential of GAs in plant protection, particularly their role in enhancing resistance to both fungal and insect attacks. The unique tetraose glycoside structure found in *Solanum commersonii* is thought to have evolved specifically to bolster the plant's defence mechanisms. High levels of tetraose GAs in *S. commersonii* correlate with increased resistance to both *Alternaria solani* and the Colorado potato beetle, making it a valuable model for further research into the immune functions of these compounds. Investigating the biosynthesis,

tissue-specific accumulation and toxicity profiles of GAs will be crucial in harnessing their full potential for agricultural applications. Understanding how structural variations in SGAs influence their potency and specificity could open new avenues for developing targeted pest and disease resistance strategies. Such approaches could significantly reduce the reliance on synthetic chemicals, promoting more sustainable and environmentally friendly pest control methods. Additionally, research by Dahlin et al. (2017) demonstrated that solanidine, the aglycone precursor of GAs, exhibits superior antifungal activity compared to its glycosylated counterparts, α-solanine and α-chaconine, particularly against *Phytophthora infestans*, the causative agent of potato late blight. Despite the expression of glycoside hydrolase genes in *P. infestans*, no evidence of deglycosylation activity has been observed, suggesting that the pathogen's ability to detoxify SGAs is limited. These findings underscore the potential of selecting for aglycone-rich SGA profiles in breeding programmes to enhance pathogen resistance in potato varieties.

The application of GAs in the food industry harbours both opportunities and significant challenges. While GAs, particularly those found in potato, have attracted attention due to their potential health benefits, their presence in food must be carefully controlled due to the risk they pose to consumer safety. Elevated concentrations of GAs in potato can lead to toxicity, which can result in adverse health effects such as gastrointestinal discomfort, neurological symptoms and, in extreme cases, even fatal poisoning. It is therefore crucial that food safety standards provide for the detection, regulation and mitigation of GA levels in potato and related products (Ruprich et al. 2009). In response to these concerns, significant efforts have been made to develop and refine methods to detect and quantify the levels of GA in potato. Technologies such as ultra-high-performance liquid chromatography coupled with mass spectrometry (UHPLC-MS/MS) have proven to be indispensable in the food industry. These advanced analytical techniques enable the precise and simultaneous identification of multiple GAs in complex potato samples and provide a reliable way to monitor their concentration (Nielsen et al. 2020). With the ability to analyse GA content at low concentrations, UHPLC-MS/MS supports stringent quality control measures and ensures that food products meet safety standards before they reach the consumer (Nie and Guo 2017). In parallel with advances in detection, researchers are exploring the bioengineering of potato varieties to reduce GA production without compromising the nutritional value or overall quality of the crop. By manipulating the biosynthetic pathways responsible for GA synthesis, scientists aim to breed potato varieties that are naturally lower in GA. This approach promises to improve food safety while maintaining the potato's desirable characteristics as a nutritious and widely consumed staple food. Aside from their potential risks, GAs also possess antimicrobial properties that have led to a growing interest in their use as natural food preservatives (Al Kabee 2019). Their ability to inhibit microbial growth could be utilised to extend the shelf life of potato-based products and reduce the need for synthetic preservatives. However, the integration of GAs into food preservation strategies requires careful consideration of safety regulations. It must be ensured that the GA content remains within safe consumption limits to avoid toxicity while realising the potential of the preservatives (Knuthsen et al. 2009). While GAs

are a double-edged sword in the food industry, their regulation and potential application in food safety and preservation are being driven by technological and genetic innovations. Ongoing research continues to explore the balance between capitalising on their benefits and mitigating the risks associated with their consumption. The future of GA application in the food industry lies in the development of safer and more reliable detection and management methods to ensure consumer health while maximising the value of the potato as a versatile and sustainable food source.

Recommendations for Managing Glycoalkaloid Accumulation in Potato

The accumulation of GAs in potato is a critical food safety issue that requires a comprehensive, evidence-based management approach. GA content is influenced by genetic predisposition, environmental variables, and post-harvest processing conditions. To curb GA biosynthesis, the potato should be stored under strictly controlled conditions, ideally at 4–6 °C in complete darkness, as elevated temperatures and exposure to light promote the formation of α-solanine and α-chaconine. Modern storage infrastructures with precise temperature and humidity control are essential for maintaining biochemical stability (Karnwal et al. 2025) In addition, innovative packaging solutions such as UV-resistant and dark materials should be used to inhibit light-induced GA synthesis. Public health measures need to raise consumer awareness of optimal storage practices and the risks associated with GA accumulation, while regulators should enforce strict storage and distribution guidelines, especially in informal markets. From a processing perspective, peeling (removal of up to 50% of GAs), thermal treatments such as boiling (15–25% reduction) and controlled frying at high temperature (up to 92% reduction) are effective prevention strategies, although frying needs to be optimised to minimise acrylamide formation. New technologies such as HPP and microbial fermentation with lactic acid bacteria are promising routes for enzymatic GA degradation without compromising nutritional value (Afaka et al. 2024; Tsikrika et al. 2021). In addition, genetic improvement initiatives should prioritise the development of low-GA potato varieties, accompanied by tailored storage protocols adapted to the susceptibility of each variety (Abbasi et al. 2016). A holistic strategy that includes genetic selection, optimised storage, advanced processing methods and strengthened regulatory policies is crucial to mitigate GA-related health risks. Strengthening interdisciplinary collaboration between agronomists, food scientists, and policy makers is key to ensuring the production and distribution of safe, high-quality, low-GA potato.

Future Research Directions

Future breeding strategies for potato should prioritise the development of varieties with reduced GA content, alongside enhanced nutritional profiles—particularly higher levels of polyphenols, carotenoids, and other bioactive compounds. The breeding process should begin with the identification and characterisation of

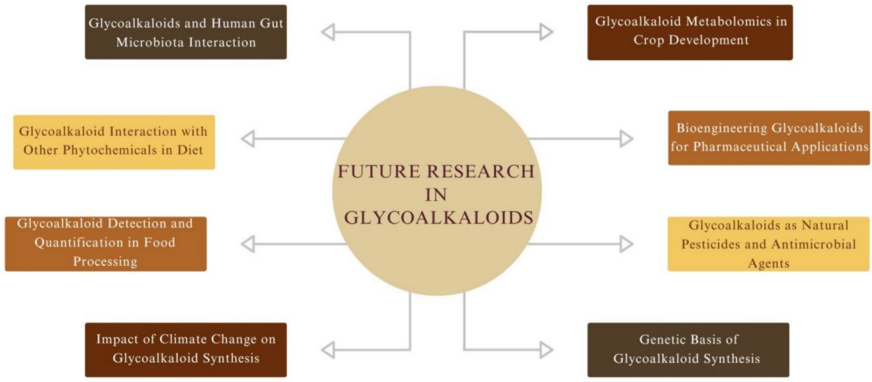

Fig. 2 Future research of glycoalkaloids in potato

genotypes that naturally exhibit low GA concentrations (Fig. 2). This is especially relevant for pigmented varieties, which are typically rich in antioxidants but may display variable GA levels. A key breeding objective must also include the development of heat-tolerant genotypes, as elevated temperatures—an increasingly frequent consequence of climate change—have been shown to stimulate GA accumulation (Gautam et al. 2024). To accelerate progress, advanced molecular breeding techniques such as marker-assisted selection (MAS), genomic selection, and quantitative trait loci (QTL) mapping should be employed to identify genetic markers associated with both low GA content and elevated levels of beneficial phytochemicals (Hasan et al. 2021; Sørensen et al. 2008; Yencho et al. 1998). These tools will enable breeders to efficiently combine desirable traits, facilitating the development of new potato varieties with improved nutritional quality and enhanced resilience to abiotic stressors (Schaart et al. 2021). In addition, breeding programmes should include controlled environmental simulations, especially under heat and drought stress conditions, to identify and select potato varieties that maintain low GA levels under difficult environmental conditions. Understanding how environmental stress affects both GA biosynthesis and nutrient composition is critical to developing varieties that perform well under different climatic conditions. Post-harvest measures should also be included in breeding programmes to assess how different storage conditions, including light and temperature, affect GA concentration and nutrient retention. Long-term field trials in different agro-climatic zones are crucial to assess the adaptability, yield and consumer acceptance of these newly developed varieties. These trials should not only investigate the effect of environmental variations on GA content, but also how long-term climatic variations may affect the growth and quality of potato. Health and safety assessments of nutrient-rich varieties with low GA content should be integrated into the breeding process to ensure that this potato is safe for human consumption (Ruprich et al. 2009). In parallel, breeding programmes should be aligned with consumer preferences through sensory evaluation studies to ensure market acceptance of healthier potato varieties. In addition, breeding strategies should focus not only on yield and nutrient composition but also on the economic

sustainability of potato production to ensure that the introduction of nutrient-rich varieties with low GA content does not compromise productivity or profitability. To deepen the understanding of GA biosynthesis, future research should focus on elucidating the molecular mechanisms that regulate GA accumulation in potato tubers (Kushwaha et al. 2025; Gan and Ling. 2022). The use of advanced "omics" technologies such as transcriptomics, proteomics, and metabolomics will allow the identification of key regulatory genes and metabolic pathways involved in GA formation. This knowledge can enable targeted genetic modifications and more precise breeding strategies to reduce GA levels. In addition, the effects of climate change on GA biosynthesis should be closely monitored, as GA synthesis pathways are likely to be altered by changing environmental conditions. Innovative post-harvest measures, such as the use of nanotechnology-based packaging materials and enzymatic degradation techniques, should be explored as potential tools to reduce GA content in processed potato products without compromising tuber quality. Research into microbial fermentation and biocontrol strategies using beneficial microorganisms could provide sustainable, non-thermal methods to mitigate GA toxicity in food.

Finally, long-term epidemiological studies are needed to better understand the health effects of chronic GA exposure in potato. These studies will help to establish clearer safety thresholds and provide regulators with the data they need to ensure safe consumption practices. Collaboration between food scientists, agronomists and regulators will be critical to translate these research findings into practical breeding applications that lead to the production of healthier, safer, and more resilient potato varieties. This comprehensive, multi-faceted approach will contribute to both food safety and the long-term sustainability of the potato industry, while meeting growing consumer demand for healthier food.

Conclusion

Over the past five decades, research on GAs has undergone a remarkable evolution, driven by technological advances and a growing understanding of their biological functions. Initial studies, limited by basic analytical techniques, focussed mainly on acute toxicity, while more recent research using advanced chromatography and mass spectrometry methods has revealed the complexity of GA biosynthesis and diversity. Despite these significant advances, challenges remain, particularly in standardising analytical methods and fully elucidating the pathways that control GA metabolism and toxicity. In addition, breeding strategies must master the difficult balance between reducing toxicity and maintaining the plant's own defence mechanisms. Although considerable progress has been made in identifying and understanding the presence, concentration and toxicity of GAs in potato, there are still some critical knowledge gaps. A thorough understanding of the genetic and environmental dynamics underlying GA traits is essential to determine how these compounds are inherited and expressed in different potato varieties. This knowledge is crucial for the development of breeding strategies that balance the maintenance of beneficial traits, such as pest resistance, with the need to minimise the toxicity of GAs in cultivated potato. To achieve this, an integrated approach is needed that considers both the ecological role of GAs in wild species and their potential impact

on human health in cultivated varieties. Such an approach is crucial for refining potato breeding programmes to ensure both agricultural sustainability and food safety. In addition, the considerable variability in GA levels across studies highlights the urgent need for standardised methods, particularly in the areas of extraction techniques and compound identification. These inconsistencies make it difficult to reliably compare results and establish general guidelines for GA content. Future research needs to focus on eliminating these methodological discrepancies while exploring the environmental and processing factors that influence GA accumulation. The application of innovative detection methods and the implementation of stringent safety protocols are essential to ensure that potato-based products are not only safe for human consumption but also offer potential health benefits. To effectively address these challenges, future research should take a multidisciplinary approach that combines advanced analytical techniques with genetic, toxicological, and agronomic studies. This comprehensive perspective will improve our understanding of GAs and address both safety concerns and their potential agricultural and health benefits. In the future, interdisciplinary collaboration that brings together expertise from analytical chemistry, plant sciences, and food safety will be crucial. Such collaboration will ensure that GA research continues to advance in a way that supports public health, agricultural sustainability, and food safety. By refining detection methods, expanding our knowledge of biosynthesis, and improving risk assessments, the scientific community can contribute to the development of safer, more nutritious, and environmentally sustainable agricultural practices.

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