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Glycoalkaloids, bitter tasting toxicants in potatoes: A review

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Abstract
Potatoes make popular dishes among humans. Currently the fresh potato consumption is decreasing and most of the potatoes are converted to value added products to meet consumer demand. Glycoalkaloids are natural bitter tasting, heat stable toxicants present in potatoes. In the edible tuber, majority of these compounds are confined to the peel. High content of glycoalkaloids impart an off flavour to the potatoes and shown to be toxic to humans and animals. There have been food safety concerns linked with the potatoes and potato based products owing to the unacceptable glycoalkaloid content in the past. Thus the glycoalkaloid content is the major determinant of the quality and safety of edible potatoes. This review highlights major areas relevant to glycoalkaloids in potatoes such as distribution and accumulation in edible tubers, factors enhancing formation, effect of various cooking methods, toxic effects and measures to minimize the content to ensure consumer safety.

Keywords: potato, glycoalkaloids, α-solanine, α-chaconine, bitter toxicants

Introduction

Potato (*Solanum tuberosum* L.), a member of the Solanaceae family, is a popular crop among different cultural back grounds. It is well grown in majority of countries and worldwide production stands in the fourth place among other major crops wheat, maize and rice [1, 2]. From year 2005 the potato production in developing countries exceeded that of the developed countries [3]. At present China contributes to the highest amount of the world's production followed by India, Russian Federation and United States [2]. It serves as a major inexpensive low fat food source rich in energy [4]. Other nutritional importance are supplementation of high quality protein, fibre and vitamins [5, 6].

The potato tuber contains a natural bitter-tasting steroidal toxicant known as glycoalkaloids [7]. These are nitrogen containing secondary metabolites present in some members of the Solanaceae family including potatoes, tomatoes and egg plants [6, 8]. Low amounts of glycoalkaloids present in commercial varieties impart the flavour to the potatoes [9]. However, potato has a bitter taste when the levels exceed 14mg/100g [5, 10].

Potato glycoalkaloids have shown to possess many health benefits such as anticancer, antimalarial, anti-inflammatory, hypoglycaemic and hypocholesterolaemic activities [5, 11, 12].

Glycoalkaloids have fungicidal and pesticidial properties and it is one of the plants natural defences [4]. Synthesis is significantly increased under unfavourable conditions, and it may serves as a stress metabolite in the potato plant [5].

This review aims to provide a comprehensive summary of the scientific literature on potato glycoalakaloids and their biological role. Since there had been reports on incidental poisoning of potatoes due to intolerable glycoalkaloid levels, practical measures documented in this review are important to improve the quality of edible tubers.

Chemical nature of glycoalkaloids in potatoes

The most important glycoalkaloids found in potato tubers are α -solanine and α-chaconine, (Figure 1) comprising about 95% of total glycoalkaloid content [1, 4, 13]. Solanine and chaconine are nitrogen containing steroidal alkaloids, bearing the same aglycone, solanidine but differ in the trisaccharide side chain [1, 9, 14]. The trisaccharide in α - solanine is galactose, glucose and rhamnose and that in α-chaconine is glucose and two rhamnose residues [1, 14]. A minor percentage of glycoakaloids (5%) contain β- solanine, γ- solanine, β-chaconine and γ-chaconine [14].

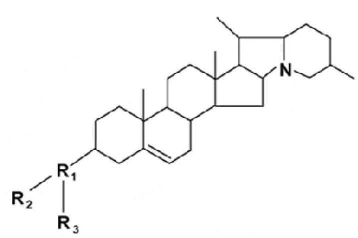

Fig 1: The structure of glycoalkaloids α -solanine and α-chaconine

(R1= β-D-galactose, R2= β-D-glucose, R3= α-L-rhamnose for α-solanine and R1= β-D-glucose, R2=R3=α-L- rhamnose for α-chaconine)

Distribution of glycoalkaloids in potato plants

Glycoalkaloid content in various parts of the plant

These compounds are distributed throughout the potato plant and the concentrations vary significantly depending on the anatomical part or the genetic variety [1, 3, 15]. A broad range for total glycoalkaloids for a given part of the plant was reported by many studies owing to considerable variation of the compound among potato plants [1, 13, 16, 17, 18]. Synthesis of glycoalkaloids occur in all parts of the plant and the highest concentrations have been reported in those parts with high metabolic rates. Flowers (215-500 mg/100g), sprouts (200-730 mg/100g) and young leaves (23-100 mg/100g) are comparatively rich in glycoalakaloids [1, 16, 17, 18].

Glycoalkaloid content in the edible tuber

Most of the edible tubers contain low amount of glycoalkaloids (less than 10 mg/100g fresh weight) [10]. The profile of glycoalkaloids in each part of the tuber was not revealed by most of the past records and the total glycoalkaloid content was reported by many such studies [1, 13, 16, 17, 18, 19, 20]. However the content of α-chaconine is reported to be slightly higher than α –solanine [13].

Glycoalkaloid content in commercial potato tubers are comparatively lower and the distribution within the tuber is not uniform. The highest levels are confined to the skin and the peel while less amounts could be observed towards the pith [13, 21]. The pith had undetectable levels of glycoalkaloids indicating that the tubers are safe to consume though there had been few reported occasions with banned levels of glycoalkaloids in tubers [3, 22, 23]. These compounds are mainly concentrated in the "eye" regions of the tuber and consumption of potatoes rich in those parts may cause potential health risks [13].

Small tubers are reported to be rich in glycoalkaloids on weight for weight basis than larger ones [1]. Green potatoes often show bitterness and this off flavour is due to the accumulation of excess amounts of glycoalkaloids in the peel [10]. Table 1 illustrates the distribution of glycoalakaloids in various tuber tissues.

Table 1: Distribution of total glycoalkaloid content in various tuber tissues of potato [16, 17, 18]

Part	Total glycoalkaloid content (mg/100g fresh weight)
Whole tuber	1-15
Skin (2-3% of tuber)	30-64
Peel (10-12% of tuber)	15-107
Flesh	1.2-10
Bitter tasting tuber	25-80
Peel from bitter tuber	150-220

Modern cultivars vs. wild progenitors

The glycoalkaloid levels in modern cultivars are much lower than in wild progenitors and this information is useful for commercial potato breeders [1]. These compounds are not transported between various parts of the plant and therefore the amount present in each part is propionate to synthesis [3]. Genetic engineering approaches could be useful for the manipulation of the level of glycoalkaloids according to commercial needs such as to reduce the levels in tubers to enhance the edibility and the safety and to increase the content in leaves to ensure the protection from diseases and predators [24].

Factors affecting levels of glycoalkaloids in the tuber

Both genetic and environmental factors have been shown to affect the levels of glycoalkaloid in potato tubers.

External factors

Environmental factors during pre-harvest period

Several external factors during pre-harvest period (soil composition and climate) and post-harvest events (effect of light, temperature, storage time, humidity, mechanical injury and sprouting) may increase the glycoalkaloid content [4, 16]. Exposure to light may stimulate chlorophyll synthesis leading to 'greening' and those tubers are reported to be rich in glycoalkaloids [25]. Extreme temperatures and dry or wet growing seasons may influence the synthesis of glycoalkaloids during growth of the plant [3, 25]. Water- logging and drought stress are other environmental factors which could enhance the production of glycoalkaloids in significant amounts in some cultivars [26, 27]. It has been reported that a double nitrogen rate during the cultivation increased glycoalkaloid content by 10% in some varieties [28]. A perusal of literature indicates that early harvested tubers may show cultivar specific impacts on glycoalkaloid accumulation than late harvested tubers [10, 23, 29].

Biodynamic conditions vs. classic cultivations

Studies conducted by Norgia *et al*., (2008) have revealed that potato breeds grown in biodynamic conditions were rich in glycoalkaloids and solanidine compared to the breeds grown in classic conditions (5-15% increase) [14]. Biodynamic conditions provide the natural environment in which potatoes could develop healthy and be able to fight against detrimental agents and therefore those varieties may have synthesized more phytorepelents. Classic cultivation of potatoes involves use of fertilizers and other chemicals according to the need and therefore those varieties are protected artificially. Hence the need of natural phytorepellents such as glycoalkaloids is less. Home Guard potato tubers had higher glycoalkaloid content and showed a little increase in response to adverse environmental conditions [26].

Factors to be considered during post-harvest period

Tubers subjected to post- harvest stress factors such as physical damage (cutting and bruising during harvest or transit), microbial or herbivore attack, improper handling and inadequate storage conditions are known factors which may influence the content of these compounds in potato tubers [30].

Tubers which are exposed to the mentioned factors if used for skin-on or peel based products have higher glycoalkaloid levels and therefore cause potential health risks. However, safe handling and monitoring of other storage conditions such as temperature and light are important to improve the quality of potatoes in commercial varieties.

Other contributing factors for glycoalkaloid synthesis

Ability to produce glycoalkaloid is inherited to potato cultivars [10, 15, 31]. This information is useful for commercial production of edible potato varieties with low content through breeding and biotechnological methodologies, while potato genotypes with high glycoalkaloid content may be developed for the pharmaceutical purposes [15]. It is recommended to grow potatoes with inherently low glycoalkaloid and to protect them from other inducers of glycoalkaloid synthesis to enhance the quality of the commercial potato destined for consumption [10]. Breeding for new varieties to obtain characteristics such as disease resistance and withstand with cold and other major changes in agricultural practices should be accompanied by careful control of the glycoalkaloid levels.

Regulatory control of the level of glycoalkaloids

The current safe level of glycoalkaloid in potatoes had set at 20mg/100g of fresh weight by several leading authorities and if the threshold value is exceeded by any cultivar, those varieties are not recommended for human consumption [32, 33]. Though the standard potato varieties with the acceptable steroidal glycoalkaloid content have released to the commercial producers for growing, occasionally the safe level could be exceeded by several environmental, physical and storage conditions as pointed out in the text. Two such reported occasions are withdrawal of potato cultivars '*Lenape*' and '*Magnum Bonum*' from United State and Swedish markets due to unacceptable glycoalkaloid levels. The reported average in '*Lenape*' was 30mg/100g and that of '*Magnum Bonum*' was 25.4/100g [3, 22, 23]. Therefore it is advisable to monitor the steroidal glycoalkaloid content when they have faced to adverse environmental conditions during the tuber bulking and also to screen the amount of these compounds in those batches before releasing them to the market as a safety precaution. Further it is recommended to assess the glycoalkaloid levels in potatoes generated from breeding programs due to the genetic transmission of undesirable levels of glycoalkaloids from wild species to hybrid progeny without which it may result in wasted effort, time and money [34].

Effect of processing on glycoalkaloid content of potatoes

Levels of glycoalkaloids in potato based products

Consumption of fried potato chips and crisps are being on the rise in most of the countries due to its attractive flavour, easy preparation and affordable price [21, 35]. Therefore recently more attention has paid to evaluate the safety of potato based products. According to Smith *et al*., (1996) potato chips (US French fries) and potato crisps (US potato chips) normally contain glycoalkaloid levels of 0.04-0.8 and 2.3-18 mg/100g product respectively [1]. Further it is reported that the skin based products such as fried skins and crisps are comparatively rich in glycoalkaloids (56.7-145 and 9.5-72 mg/100g product respectively) [1]. Jacket potatoes and more recently skin based preparations (potato crisps) have shown a relatively high content of glycoalkaloids [1] According to the reports by Mondy and Gosselin, (1988) "salt potatoes" (small whole potatoes) are popular dishes among the consumers of the North Eastern United State due to the belief that the peel contains more nutrients [22]. Further, according to the documentary evidence by, potatoes are processed with peel into fried snack foods such as potato chips and kettle chips by some Asian countries and may lead to ingestion of toxic glycoalkaloids [33, 36].

Loss of glycoalkaloids during production of potato based Products

Production of French fries from potatoes involve several steps such as cutting, blanching, drying and frying [35]. During the production chain, the highest amount of glycoalkaloids were removed during peeling, blanching and frying and the French fries ready for consumption contained 3-8% of glycoalkaloids compared to raw material [35]. Similar findings have been obtained by a study carried out to evaluate the quality of French fries by Tajner-Czopek *et al*., (2008) and reported that the highest decrease in glycoalkaloids was caused by frying, which is the final step of processing (97.5% loss when compared to raw unpeeled potatoes) [37]. The average loss during other preliminary steps were 50%, 53% and 58% in peeling, cutting and blanching respectively [38]. The level of glycoalkaloids in potato granules were evaluated by Rytel (2012) and reported that the highest decrease in glycoalkaloids were caused by peeling (50%) and blanching (63%) and the finished product had only 14% of the initial quantity [38].

Effect of in-home cooking methods on glycoalkaloid content

Several studies suggest that peeling usually removes most of the glycoalkaloids in the edible tubers. Sinden and Deahl (1976) reported that up to 60% of the total glycoalkaloids in whole tubers were removed with the peel [10]. Mondy and Gosellin reported that potatoes cooked with peel were bitterer than unpeeled potatoes due to the migration of glycoalkaloids into the cortex during the cooking process, though they are less mobile [22]. Similar findings have been obtained by Tajner-Czopek *et al*., (2014) and the authors further claimed that peeling removes higher amount of glycoalkaloids (approximately twice) than cooking [37]. Bushway and Ponnampalam (1981) investigated the stability of glycoalkaloids during four cooking procedures; frying, baking, microwaving and boiling [39]. A slight loss of glycoalkaloids was shown by frying whereas the other cooking methods which were tested did not significantly reduce the glycoalkaloid content. In a similar study, it was reported that the potato glycoalkaloids are relatively stable under normal home cooking conditions revealing that only little reduction was shown by boiling and microwave treatment [40]. The study further suggested that the critical temperature for decomposition of glycoalkaloids in potatoes may be around 170° C based on the results obtained by using deep frying at different temperatures (157°C, 170 °C and 260°C) [40].

Studies done to evaluate the effect of various processing methods suggest that the glycoalkaloids are relatively stable under conventional cooking procedures. In typical household preparations, many Asians including Sri Lankans peel off the potatoes after boiling. These compounds migrate into the internal tissue of the tuber during boiling and therefore conventional method of boiling reduces the quality of edible potatoes. Thus it is advisable to remove the peel of the tubers before any cooking process to reduce glycoalkaloids and to improve the quality [40].

Toxicity caused by glycoalkaloids in potatoes

It is important to be aware on toxicity caused by potato glycoalkaloids due to following reasons.

1. The potato makes a part of the regular diet of majority of the people worldwide.

2. The concentration of glycoalkaloids present in potato has a major economic impact on potato breeders since the potato varieties exceeding the level of 20mg/100g fresh weight is probably a rejection criteria in marketing [3, 22, 23].
3. According to the reported data by Smith *et al*. (1996), modern preparations such as skin based products (crisps and fried skins) may contain unacceptable levels of glycoalkaloids (up to 72 mg/100g in crisps and 145 mg/100g in skin based products) and ingestion may elicit health problems in humans [1]. A review of toxicological literature by Zeiger (1998) reported that baked and fried potato peels are a major source of large quantities of α -solanine and α-chaconine in the diet [41].

Published toxicological findings on humans

The documented history of the steroidal glycoalkaloid poisoning from potatoes extend up to year 1917 from Britain on an outbreak of solanine poisoning by a hotel proprietor [42]. Baked potatoes with skins were identified as the causative agent and the victims showed vomiting, diarrhoea and abdominal pain [42]. A clinical observation was recorded by Unverricht (1937) on an outbreak of sickness among agricultural workers in a village near by Beriln [43]. Excluding potatoes from the diet resolved the symptoms confirming that the potatoes could be the causative agents for the illness. Mc Millan and Thompson (1979) have reported an incidence of poisoning among school boys caused by ingestion of potatoes which had high amounts of α-solanine and α- chaconine [44]. Cumulative assessment of toxicological data suggests that these compounds are toxic to humans at a very lower dose when compared with other animal models [4].

Biological activities of glycoalkaloids

General symptoms of glycoalkaloid poisoning in humans are nausea, vomiting, diarrhoea, stomach and abdominal cramps, headache, fever, rapid and weak pulse, rapid breathing and hallucination [3, 14]. Coma and death has been resulted in more serious cases [1, 3]. There are two main biological functions of glycoalkaloids [1, 3]. The first is their ability to bind with the membrane sterols and there by cause the disruption of the membrane architecture leading to leakage of cellular contents raising gastrointestinal disturbances such as abdominal cramps, vomiting and diarrhoea [1, 4, 45]. Differential diagnosis of glycoalkaloid poisoning is complicated since the symptoms of acute intoxication share common features of other gastro intestinal disorders [1]. The other major biological action of glycoalkaloid is the inhibition of acetylcholine esterase, the enzyme involved in the hydrolysis of the neurotransmitter acetylcholine at the cholinergic synapses. The anti-acetylcholine esterase activity of glycoalkaloids is manifested by neurological symptoms such as weakness, confusion and depression [46].

Absorption vs. excretion

Absorption of potato glycoalkaloids in humans are apparently proportional to the amount ingested [47]. An overview on the toxicology of solanine (the major glycoalkaloid in potato) compiled by Dalvi and Bowie (1983) revealed that solanine when ingested is less toxic compared to the parenterally administered solanine due to its poor absorption, rapid excretion and conversion into less toxic secondary metabolites in the stomach [48]. A controversial opinion regarding the clearance of glycoalkaloids from the human body was reported by Mensinga *et al*. in 2005 [49]. However, this ascending dose study with human volunteers showed that the clearance of glycoalkaloids from the body takes more than 24 hours and further suggested that there is a possibility of accumulating the toxicants in case of daily consumption. The observation by Mensinga *et al*. (2005) was further confirmed by Nishie *et al*. (1971) reporting that once it is in the blood stream, excretion appears to be low indicating that the compounds might accumulate in various organs in the body including liver by using animal models [49, 50].

Safe level of intake

Poisoning caused by glycoalkaloids on humans is subjected to individual variations [1]. The toxic dose of glycoalkaloids in humans is 1-5 mg/Kg body weight and lethal dose is 3-6 mg/Kg body weight when administered through the oral route [1]. Therefore the USDA and other leading authorities have defined a glycoalkaloid level of 20 mg/100g fresh weight and 100mg/100g dry weight as the safe limit in edible tubers [1, 3, 33]. Analysis of the toxicological data on human subjects failed to establish a safe level of intake and further indicated that a considerable effort is required to work out on such a cut off value [13]. Due to variations of the glycoalkaloid content according to pre harvest and post-harvest factors and the individual variations of the toxic dose, it has been proposed that the safety limit has to be brought down to a level less than the recommended [20]. Commercial varieties tend to have glycoalkaloid content less than the accepted safety limit of 20 mg/100g fresh weight [1]. It has been shown that the potato tubers exceeding the glycoalkaloid level of 14mg/100g had bitterness while a burning sensation in throat and mouth was caused by tubers exceeding 22mg/100g [32]. Therefore the quantity of glycoalkaloids present in edible tubers has a direct impact on the quality of tubers. Since the off flavours caused by high glycoalkaloid content will reduce the commercial value of tubers, routine testing for glycoalkaloids are necessary for the edible tubers and for potato based products to ensure the safety of the consumer.

Published findings on animal experiments

Several laboratory experiments have shown that the glycoalkaloids are toxic to animal models such as Syrian Golden hamsters, rabbits, rats and mice [50, 51, 52, 53]. Experimental studies by Nishie *et al*. (1971) further confirmed that the toxicological potency of the agyclone (solanidine) was less when compared that with the solanine revealing that the potential toxicity is mediated by the carbohydrate side chains of the two compounds, α -solanine and α-chaconine [50]. The acute toxicity studies have revealed that the LD_{50} for solanine in mice is 32.3 mg/Kg BW and that of chaconine is 19.2 mg/Kg BW [13]. Oral administration of solanine to mice showed less toxic effects (oral LD50 ≥1000 mg/KgBW) when compared with that of the parenteral administration [47]. Rats exhibited a comparatively higher toxic dose for solanine and chaconine (65.6-107.5 mg/KgBW) when administered intra peritonially [14]. Animal experiments suggest that α-chaconine is more toxic than α-solanine [20, 50].

Measures to optimize the safety of edible tubers

Based on the scientific evidences, following recommendations (Table 2) would be helpful for farmers and commercial producers, retail sellers and consumers to improve the quality of edible potatoes.

Table 2: Strategies for controlling glycoalkaloid formation/accumulation in potatoes and potato products

	Intervention
Farmers and commercial producers	Selection of cultivars low in glycoalkaloids Careful manipulation of environmental factors (low temperature, desired soil nitrogen content) Minimization of damage to tubers during post- harvest handling Screening for glycoalkalod content of new varieties prior to market release
Retail sellers	Packing in opaque plastic films or paper bags (to protect from light) Rotate the stocks in retail displays Store in a shaded, cold environment
Consumers	Selection of intact tubers of moderate/large size Peel off the tuber before any processing method Eliminate use of tubers with bitter taste and green colour

Conclusion

Potatoes, as a staple for humans have shown to be safe throughout the long history of consumption despite the presence of bitter tasting toxicants. Fortunately most of the commercial potato varieties contain a glycoalkaloid level less than 20mg/100g fresh weight (the acceptable upper safety limit) in edible tubers. Processed potato products have increased in popularity and therefore, from a food safety perspective it is important that farmers and retailers review their cultural and marketing practices in order to ensure that the tubers contain a safe level of glycoalkaloids from the field through storage and retail outlets to the table. In addition selection criteria and processing methods adopted by consumers are important to ensure the safety of edible tubers.

Declaration of interest

The author reports no conflicts of interest.

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