TITLE: Effect of genotype and environment on the glycoalkaloid content of rare, heritage and commercial potato varieties

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Effect of genotype and environment on the glycoalkaloid content of rare, heritage and commercial potato varieties

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Short title: Effect of genotype and environment on the (…)

ABSTRACT

Potatoes accumulate toxic steroidal compounds that could be harmful for humans if consumed in high quantities and must be controlled. In this study we were interested in assessing the levels and variation of glycoalkaloid content in sixty varieties of potato planted in two trial sites over two years.

Total glycoalkaloid levels ranged from 4 to 957 mg kg^{-1} of dry weight in the flesh and from 150 to 8133 mg kg^{-1} in the skin, with the latter accumulating generally more α-chaconine than α-solanine. Contents in the flesh were below the safe limit for all varieties, but were generally above in the skin. Maximum values in each site and year of cultivation were found for varieties 'Beauty of Hebron', 'May Queen' and 'Arran Pilot' in the skin and 'Beauty of Hebron', 'International Kidney' and 'Congo' in the flesh. Year of cultivation had a significant effect on total glycoalkaloid content ($p<0.0001$), with interactions between variety and site of cultivation and variety and year of cultivation also significant ($p<0.0001$), implying that environmental effects

seem to act differentially and could induce high levels in genetically predisposed varieties.

Keywords: potato, glycoalkaloids, α-solanine, α-chaconine, *Solanum tuberosum* L.

Practical application: This paper reports the levels of toxic glycoalkaloids in sixty varieties of potato. Dietary intake and safety of consumers is discussed and varieties used by the potato processing industry are assessed in terms of safety and potential use of waste peel as raw material.

INTRODUCTION

Glycoalkaloids are secondary metabolites produced by plants of the Solanaceae family, which includes edible plants such as potato (*Solanum tuberosum* L.), tomato (*Lycopersicon esculentum*), eggplant (*Solanum melongena*) or peppers (*Capsicum annum*). They are toxic compounds involved in plant protection against pests and diseases and can also be potentially harmful for humans if consumed in high quantities. The characteristic potato flavour seems to be related to these compounds, although glycoalkaloids can cause bitterness and a burning sensation in the mouth at high levels (Friedman 2006). These unpleasant sensations make poisoning episodes scarce, although a few cases have been reported (Willimott 1933; McMillan and Thompson 1979).

The toxicity of glycoalkaloids appears to be related to their anticholinesterase activity and disruption of cell membranes, producing respectively neurological disorders and gastrointestinal disturbances (Milner and others 2011). The safe acute oral dose in humans is considered to be 1mg kg^{-1} body mass and the acute toxic dose 2-5 mg kg^{-1} body mass, with 3-6 mg kg^{-1} body mass potentially lethal (Koleva and others 2012). It is commonly accepted that levels above 200 mg kg^{-1} in fresh potato are not safe (Smith and others 1996). Besides acute intoxication, little is known about subacute or chronic effects. Studies have linked glycoalkaloids to intestinal damage in animal models (Langkilde and others 2009; Iablokov and others 2010). It has also been suggested that they may be involved in the higher incidence of inflammatory bowel conditions in Western countries (El-Tawil 2008). Glycoalkaloids seem to remain in the body for more than 24 hours after ingestion, which makes long term effects possible in daily potato consumers (Mensinga and others 2005).

Chemically, glycoalkaloids consist of an alkaloid bound to an oligosaccharide. In commercial potatoes, the major glycoalkaloids, α-solanine and α-chaconine, consist of the aglycone solanidine attached to a trisaccharide: galactose, glucose and rhamnose in α-solanine and glucose, rhamnose and rhamnose in α-chaconine. Both forms account for more than 95% of the total glycoalkaloid content in cultivated varieties. α-Chaconine is more toxic than α-solanine, however, the overall toxicity depends not only on the levels of both compounds but also on their ratio, since they produce synergistic effects when present in the same tissue (Nema and others 2008).

Despite the status of glycoalkaloids as potentially dangerous components of potatoes, beneficial effects have also been reported. *In vitro* assays produced positive results against several types of cancer (Lee and others 2004; Friedman and others 2005; Yang and others 2006; Shih and others 2007), and potato glycoalkaloids and peel extracts have shown anti-inflammatory activity (Kenny and others 2013). In experiments with mice, several glycoalkaloids were active against malaria (*Plasmodium yoelii)*, particularly α-chaconine (Chen and others 2010), and both α-solanine and α-chaconine seemed to protect mice against *Salmonella typhimurium* (Gubarev and others 1998). Furthermore, potato glycoalkaloids could be used as raw materials for the production of steroid hormones. Solanidine can be released from α-solanine or α-chaconine by enzymatic or acid hydrolysis and used as a substrate for synthesis (Schieber and Saldaña 2009).

A variety of factors can influence the formation of glycoalkaloids, such as growing, storage and transportation conditions, genotype, temperature, cutting, sprouting and exposure to phytopathogens and light (Friedman 2006). In potatoes, the majority of the glycoalkaloids are found in the outer layers of the tuber, with increased concentrations around the eyes and injuries and in the sprout (Friedman and others 2003; Nema and others 2008). Peeling the tuber removes 20% to 58% of the total glycoalkaloids (Tajner-Czopek and others 2008; Tajner-Czopek and others 2012), whereas cooking has variable effects. Glycoalkaloids are very heat stable, with α-solanine decomposing at temperatures between 260 and 270ºC (Porter 1972). Boiling or microwaving whole tubers does not seem to decrease the glycoalkaloid content (Mulinacci and others 2008), but boiling peeled potatoes produces a reduction of about 39% (Tajner-Czopek and others 2012). Frying is the most effective method of lowering the levels of glycoalkaloids, with reported differences between raw, peeled and fried potatoes of 77 to 94% (Pęksa and others 2006; Tajner-Czopek and others 2012).

Glycoalkaloids may pose a risk for potato consumers and therefore their levels must be controlled, but they can also be potentially valuable raw materials, in particularly the peel waste of the potato industry. With the aim of providing valuable information on the effects of genotype and environment in the levels of these compounds, we determined the contents of α-solanine and α-chaconine in the skin and the flesh of a wide range of varieties of potato and estimated the total glycoalkaloid content in both tissues.

MATERIALS AND METHODS

Plant materials

To assess the effects of environmental factors in the levels of glycoalkaloids, sixty varieties of potato were cultivated in 2010 at two different locations in the Republic of Ireland and at one location in 2011. Seed tubers were planted in May in Carlow (52.858883,-6.916366), in 2010 and 2011, and in Duleek Co. Meath (53.655825,-6.41578) in 2010, with three and two replicates respectively, following an alpha block design. Fertilizer was applied as calcium ammonium nitrate (CAN), single super-phosphate and sulphate of potash according to Teagasc recommendations (Coulter and Lalor 2008). Weed and pest control treatments were in accordance with Integrated Pest Management strategies typical of Irish potato production using approved pesticides (Pesticide Control Service - 2013). Mature tubers were harvested in October 2010 and 2011 after 5 months of growth. Tubers of the most similar size possible were selected for analysis, washed and stored at 4ºC while sample preparation was being carried out.

Sample preparation

For each cultivar, composite samples were prepared pooling two to twelve tubers, depending on their size, from the same plant. Tubers were peeled with a potato peeler, the flesh of each tuber quartered from stem to bud end and one of the quarters sliced. Skin and flesh tissues were vacuum sealed, snap frozen at -40ºC and stored at -20ºC until they were freeze-dried. Freeze-dried samples were ground to a fine powder using a coffee grinder (Krups F203) and stored at -20ºC until analysis.

Glycoalkaloids extraction and analysis

Glycoalkaloids were determined according to Knutshen (2009) with slight modifications.

Extraction of glycoalkaloids from freeze-dried tissue (1 g of skin or 7 g of flesh) was carried out in 50 ml polypropylene centrifuge tubes with 20 ml of an extraction solution consisting of ultra-pure water, acetic acid (Sigma-Aldrich, Wicklow, Ireland) and sodium hydrogen sulfite (Acros Organics, Geel, Belgium) in proportions 100:5:0.5 v:v:w respectively. The tubes were shaken for 15 min at 500 rpm, and centrifuged at 4137 g for 10 min. The supernatants were transferred to 15 ml polypropylene tubes and centrifuged again for 4 min at 1486 g and 4ºC. The supernatants were collected and stored at 4ºC until analysis.

Clean-up of the extracts was carried out with Thermo Hypersep C18, 500 mg Solid Phase Extraction (SPE) columns (Thermo Scientific, Hertfordshire, UK). The columns were conditioned with 5 ml of acetonitrile (Sigma, Wicklow, Ireland) followed by 5 ml of the extraction solution specified above. A volume of 10 ml of sample extract was passed through the column, washed with 4 ml of 15% acetonitrile and the analytes eluted with 4 ml of HPLC mobile phase. This consisted of acetonitrile and 0.01M phosphate buffer pH 7.6 in proportions 50:50 v:v. The eluate was collected in 5 ml volumetric flasks and made up to volume with mobile phase. All sample solutions were filtered through 0.45 μm PTFE syringe filters (Whatman, Kent, UK) prior to chromatographic analysis.

Chromatography was carried out using a Shimazdu HPLC system (Shimadzu Corp. Nakagyo-ku, Kyoto, Japan). A volume of 20 μl of sample or standard was injected onto a Zorbax C18, 5 μm, 4.6x150 mm column fitted with a C18 precolumn (Agilent, Cork, Ireland), and separated at 30ºC by isocratic elution with the mobile phase specified above at a flow rate of 1.5 ml/min. Detection was made at 202nm.

Identification of α-solanine and α-chaconine was based on comparison of retention times and by spiking samples with known amounts of pure standards (α-solanine standard, Sigma-Aldrich, Wicklow, Ireland; α-chaconine standard, Extrasynthese, Genay Cedex, France). In the chromatogram of flesh samples two additional peaks appeared before α-solanine and after α-chaconine (Fig 1). To rule out the possibility that these two peaks were glycoalkaloid degradation products, hydrolysis of α-solanine and α-chaconine standards was carried out. Methanol (Sigma, Wicklow, Ireland) and 0.2M HCl (Applichem, Dublin, Ireland) were mixed with each standard and left reacting at 65ºC; α-solanine was left for 300 min. and α-chaconine for 1100 min. None of the degradation products of α-solanine or α-chaconine matched the retention times of the unknown peaks in the samples, so it was concluded that they were not α-solanine or α-chaconine derivatives and were not quantified.

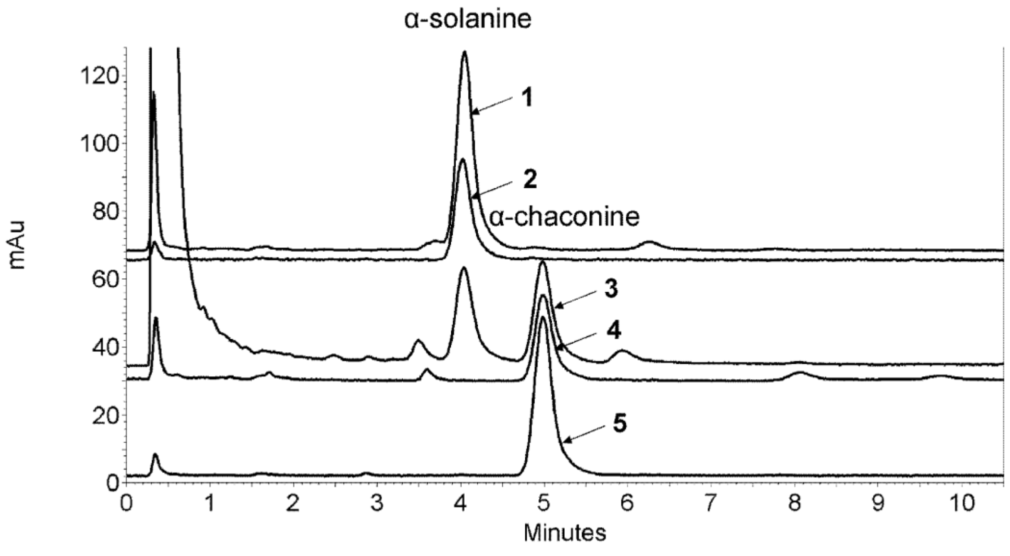

Figure 1. HPLC chromatograms. From top to bottom: **(1)** α-solanine standard hydrolized for 300 min, **(2)** α-solanine standard, **(3)** flesh sample, **(4)** α-chaconine standard hydrolized for 1100 min and **(5)** α-chaconine standard.

Quantification was made by external calibration. Stocks of each glycoalkaloid standard were prepared in methanol and an aliquot of both stock solutions mixed, dried under a nitrogen stream at 40ºC and re-dissolved in mobile phase. The concentrations of α-solanine and α-chaconine in the extracts were calculated by comparison with the areas of known amounts of the standards. Results were expressed as mg of α-solanine or α-chaconine per kg of dried sample (DW). Total glycoalkaloid content was calculated by adding the amounts of α-solanine and α-chaconine.

Statistical analysis

The data across sites was normalized using natural logarithms and subjected to analysis of variance. Statistical analysis was carried out with SAS 9.1.3. (Cary, NC) using a generalized linear mixed model allowing for multiple comparisons with Tukey adjustment. For the sake of clarity, errors associated with mean values for each variety were not included in the tables. However, the confidence limits (95% confidence level) were between 38 and 128% of each mean value for α-solanine and between 33 and 99% for α-chaconine.

RESULTS AND DISCUSSION

Total glycoalkaloid content in the skin and flesh of tubers included in this study showed considerable variation, ranging from 4 to 957 mg kg^{-1} DW in the flesh and from 150 to 8133 mg kg^{-1} DW in the skin (Tables 1 and 2). Variety 'Beauty of Hebron' had the highest total glycoalkaloid content in the tubers grown in Duleek in 2010 in both skin and flesh tissues, with 6542 and 577 mg kg^{-1} DW respectively. In Carlow in 2010, the highest levels were found in variety 'May Queen' in the skin and variety 'International Kidney' in the flesh, reaching values of 8133 and 957 mg kg^{-1} DW respectively. Maximum contents for tubers grown in Carlow in 2011 were variety 'Arran Pilot' in the skin, with 4291 mg kg^{-1} DW, and variety 'Congo' in the flesh, with 412 mg kg^{-1} DW (Tables 1 and 2). Pooling the data from the three cultivation sites, the skin of potato tubers accumulated 21 times more glycoalkaloids than the flesh. Total glycoalkaloids in each of the tissues were positively correlated, with a Pearson's coefficient of 0.533 ($p<0.0001$).

Table 1. α-solanine, α-chaconine, total glycolakaloid content (α-solanine + α-chaconine) and ratio of α-chaconine:α-solanine in the skin of sixty potato varieties grown at two locations in Ireland over two years. Results expressed as mg kg^{-1} DW.

variety	skin colour	Carlow 2010				Carlow 2011				Duleek 2010			
		α-solanine (A)	α-chaconine (B)	total (A+B)	ratio (B/A)	α-solanine (A)	α-chaconine (B)	total (A+B)	ratio (B/A)	α-solanine (A)	α-chaconine (B)	total (A+B)	ratio (B/A)
May Queen	Y	4108 [a]	4025 [a]	8133	1.0	1449 [a,b,c,d,e]	1880 [a,b,c,d,e,f,g]	3330	1.3	1649 [a,b,c,d,e]	2469 [a,b,c,d,e]	4118	1.5
Beauty of Hebron	P	3440 [a]	3445 [a]	6885	1.0	*1691 [a,b,c,d,e]	*1832 [a,b,c,d,e,f,g,h]	3523	1.1	3081 [a,b]	3461 [a]	6542	1.1
Craigs Royal	PR	3488 [a]	2832 [a,b,c]	6320	0.8	1283 [a,b,c,d,e]	1182 [a,b,c,d,e,f,g,h,i,j]	2465	0.9	2462 [a,b,c,d]	2068 [a,b,c,d,e,f,g]	4531	0.8
Eersterling	Y	3055 [a,b]	2871 [a,b,c]	5926	0.9	1937 [a,b,c,d]	1859 [a,b,c,d,e,f,g]	3796	1.0	2924 [a,b,c]	2703 [a,b,c,d,e]	5627	0.9
Axona	R	1823 [a,b,c,d]	2932 [a,b]	4755	1.6	1144 [a,b,c,d,e]	1871 [a,b,c,d,e,f,g]	3015	1.6	1668 [a,b,c,d,e]	2826 [a,b,c,d]	4494	1.7
Russett Burbank	Y	*2343 [a,b,c,d]	*2236 [a,b,c,d,e,f]	4579	1.0	653 [a,b,c,d,e,f,g]	912 [a,b,c,d,e,f,g,h,i,j,k]	1564	1.4	1595 [a,b,c,d,e]	1843 [a,b,c,d,e,f,g,h]	3438	1.2
Flourball	Y	*2338 [a,b,c,d]	*2204 [a,b,c,d,e,f,g]	4542	0.9	1445 [a,b,c,d,e]	1462 [a,b,c,d,e,f,g,h,i,j]	2908	1.0	3169 [a,b]	2599 [a,b,c,d,e]	5768	0.8
Arran Pilot	Y	1914 [a,b,c,d]	2362 [a,b,c,d,e]	4277	1.2	*1771 [a,b,c,d,e]	*2520 [a,b,c,d,e]	4291	1.4	1876 [a,b,c,d]	2895 [a,b,c]	4771	1.5
Sharpes Express	Y	2037 [a,b,c,d]	2206 [a,b,c,d,e,f]	4243	1.1	1478 [a,b,c,d,e]	1555 [a,b,c,d,e,f,g,h,i,j]	3033	1.1	1761 [a,b,c,d,e]	1990 [a,b,c,d,e,f,g]	3750	1.1
Arran Chief	W	1729 [a,b,c,d,e]	2290 [a,b,c,d,e,f]	4019	1.3	*536 [a,b,c,d,e,f,g,h]	*910 [a,b,c,d,e,f,g,h,i,j,k]	1446	1.7	849 [a,b,c,d,e,f,g]	1402 [a,b,c,d,e,f,g,h,i,j]	2251	1.7
British Queen	Y	1766 [a,b,c,d,e]	2200 [a,b,c,d,e,f,g]	3965	1.2	*1099 [a,b,c,d,e,f]	*1372 [a,b,c,d,e,f,g,h,i,j]	2471	1.2	–	–	–	–
Druid	W	1863 [a,b,c,d]	2015 [a,b,c,d,e,f,g]	3878	1.1	1058 [a,b,c,d,e,f]	1323 [a,b,c,d,e,f,g,h,i,j]	2381	1.3	1289 [a,b,c,d,e]	1466 [a,b,c,d,e,f,g,h,i,j]	2755	1.1
Edgecote purple	B	*1496 [a,b,c,d,e]	*2345 [a,b,c,d,e,f]	3841	1.6	*812 [a,b,c,d,e,f,g]	*1457 [a,b,c,d,e,f,g,h,i,j]	2268	1.8	2106 [a,b,c,d]	3033 [a,b]	5138	1.4
Lady Claire	Y	1502 [a,b,c,d,e]	2278 [a,b,c,d,e,f]	3780	1.5	1072 [a,b,c,d,e,f]	1668 [a,b,c,d,e,f,g,h,i]	2740	1.6	1902 [a,b,c,d]	3149 [a,b]	5051	1.7
Edzell Blue	B	1632 [a,b,c,d,e]	2053 [a,b,c,d,e,f,g]	3685	1.3	1196 [a,b,c,d,e]	1356 [a,b,c,d,e,f,g,h,i,j]	2552	1.1	1023 [a,b,c,d,e,f]	1438 [a,b,c,d,e,f,g,h,i,j]	2462	1.4
Nicola	Y	1302 [a,b,c,d,e]	2251 [a,b,c,d,e,f]	3553	1.7	707 [a,b,c,d,e,f,g]	1421 [a,b,c,d,e,f,g,h,i,j]	2128	2.0	1144 [a,b,c,d,e]	2096 [a,b,c,d,e,f,g]	3240	1.8
Burren	Y	1288 [a,b,c,d,e]	2073 [a,b,c,d,e,f,g]	3361	1.6	777 [a,b,c,d,e,f,g]	1160 [a,b,c,d,e,f,g,h,i,j]	1937	1.5	878 [a,b,c,d,e,f,g]	1617 [a,b,c,d,e,f,g,h,i]	2495	1.8
Lady Rosetta	R	*1597 [a,b,c,d,e]	*1676 [a,b,c,d,e,f,g,h,i]	3273	1.0	536 [a,b,c,d,e,f,g,h]	643 [a,b,c,d,e,f,g,h,i,j,k,l]	1180	1.2	1394 [a,b,c,d,e]	1327 [a,b,c,d,e,f,g,h,i,j]	2721	1.0
Collen	Y	1342 [a,b,c,d,e]	1688 [a,b,c,d,e,f,g,h,i]	3030	1.3	927 [a,b,c,d,e,f,g]	1228 [a,b,c,d,e,f,g,h,i,j]	2155	1.3	1305 [a,b,c,d,e]	1638 [a,b,c,d,e,f,g,h,i]	2943	1.3
Lewis black	B	1520 [a,b,c,d,e]	1448 [a,b,c,d,e,f,g,h,i,j]	2968	1.0	260 [d,e,f,g,h,i]	350 [i,j,k,l,m]	609	1.3	619 [a,b,c,d,e,f,g]	746 [a,b,c,d,e,f,g,h,i,j,k,l]	1365	1.2
Early Rose	R	928 [a,b,c,d,e,f,g]	2008 [a,b,c,d,e,f,g]	2936	2.2	*816 [a,b,c,d,e,f,g]	*1742 [a,b,c,d,e,f,g,h,i]	2558	2.1	1067 [a,b,c,d,e,f]	2591 [a,b,c,d,e]	3657	2.4
Harlequin	PR	1122 [a,b,c,d,e,f]	1743 [a,b,c,d,e,f,g,h,i]	2864	1.6	639 [a,b,c,d,e,f,g]	1209 [a,b,c,d,e,f,g,h,i,j]	1848	1.9	1303 [a,b,c,d,e]	1947 [a,b,c,d,e,f,g]	3250	1.5
Duke of York	R	1031 [a,b,c,d,e,f]	1736 [a,b,c,d,e,f,g,h,i]	2767	1.7	461 [a,b,c,d,e,f,g,h]	702 [a,b,c,d,e,f,g,h,i,j,k,l]	1163	1.5	601 [a,b,c,d,e,f,g]	1005 [a,b,c,d,e,f,g,h,i,j,k]	1606	1.7
Charlotte	Y	1333 [a,b,c,d,e]	1415 [a,b,c,d,e,f,g,h,i,j]	2748	1.1	1431 [a,b,c,d,e]	1581 [a,b,c,d,e,f,g,h,i]	3012	1.1	2679 [a,b,c,d]	2780 [a,b,c,d]	5458	1.0
King Edward	PR	1083 [a,b,c,d,e,f]	1626 [a,b,c,d,e,f,g,h,i]	2709	1.5	439 [b,c,d,e,f,g,h,i]	870 [a,b,c,d,e,f,g,h,i,j,k]	1310	2.0	954 [a,b,c,d,e,f,g]	1570 [a,b,c,d,e,f,g,h,i,j]	2524	1.6
Kerrs Pink	R	952 [a,b,c,d,e,f,g]	1739 [a,b,c,d,e,f,g,h,i]	2691	1.8	–	–	–	–	801 [a,b,c,d,e,f,g]	1638 [a,b,c,d,e,f,g,h,i]	2439	2.0
Pink Fir Apple	P	995 [a,b,c,d,e,f,g]	1560 [a,b,c,d,e,f,g,h,i,j]	2556	1.6	920 [a,b,c,d,e,f,g]	1256 [a,b,c,d,e,f,g,h,i,j]	2175	1.4	1151 [a,b,c,d,e]	1630 [a,b,c,d,e,f,g,h,i]	2780	1.4
Ulster Sceptre	W	1164 [a,b,c,d,e]	1337 [a,b,c,d,e,f,g,h,i,j]	2501	1.1	615 [a,b,c,d,e,f,g]	886 [a,b,c,d,e,f,g,h,i,j,k]	1501	1.4	694 [a,b,c,d,e,f,g]	1028 [a,b,c,d,e,f,g,h,i,j,k]	1722	1.5
Pentland Ivory	Y	1259 [a,b,c,d,e]	1179 [a,b,c,d,e,f,g,h,i,j]	2438	0.9	*707 [a,b,c,d,e,f,g]	*526 [c,d,e,f,g,h,i,j,k,l,m]	1233	0.7	1368 [a,b,c,d,e]	1313 [a,b,c,d,e,f,g,h,i,j]	2681	1.0
International Kidney	Y	1263 [a,b,c,d,e]	1116 [a,b,c,d,e,f,g,h,i,j]	2379	0.9	763 [a,b,c,d,e,f,g]	669 [a,b,c,d,e,f,g,h,i,j,k,l]	1432	0.9	864 [a,b,c,d,e,f,g]	1262 [a,b,c,d,e,f,g,h,i,j]	2127	1.5

(continued)

Table 1 - Continued.

variety	skin colour	Carlow 2010				Carlow 2011				Duleek 2010			
		α-solanine (A)	α-chaconine (B)	total (A+B)	ratio (B/A)	α-solanine (A)	α-chaconine (B)	total (A+B)	ratio (B/A)	α-solanine (A)	α-chaconine (B)	total (A−B)	ratio (B/A)
Home Guard	Y	811 ^{a,b,c,d,e,f,g}	1551 ^{a,b,c,d,e,f,g,h,i,j}	2363	1.9	*611 ^{a,b,c,d,e,f,g}	*1117 ^{a,b,c,d,e,f,g,h,i,j}	1728	1.8	931 ^{a,b,c,d,e,f,g}	1639 ^{a,b,c,d,e,f,g,h,i}	2570	1.8
Sarpo Mira	Y	1116 ^{a,b,c,d,e,f}	1178 ^{a,b,c,d,e,f,g,h,i,j}	2293	1.1	538 ^{a,b,c,d,e,f,g,h}	641 ^{a,b,c,d,e,f,g,h,i,j,k,l}	1179	1.2				
Pimpernell	R	764 ^{a,b,c,d,e,f,g}	1493 ^{a,b,c,d,e,f,g,h,i,j}	2257	2.0	642 ^{a,b,c,d,e,f,g}	1068 ^{a,b,c,d,e,f,g,h,i,j,k}	1710	1.7	–	–	–	–
Bionica	Y	1111 ^{a,b,c,d,e,f}	1126 ^{a,b,c,d,e,f,g,h,i,j}	2237	1.0	*513 ^{a,b,c,d,e,f,g,h}	*632 ^{a,b,c,d,e,f,g,h,i,j,k,l}	1145	1.2	1176 ^{a,b,c,d,e}	1314 ^{a,b,c,d,e,f,g,h,i,j}	2490	1.1
Ambo	PR	*940 ^{a,b,c,d,e,f,g}	*1243 ^{a,b,c,d,e,f,g,h,i,j}	2183	1.3	797 ^{a,b,c,d,e,f,g}	1306 ^{a,b,c,d,e,f,g,h,i,j}	2103	1.6	643 ^{a,b,c,d,e,f,g}	1056 ^{a,b,c,d,e,f,g,h,i,j,k}	1700	1.6
Arran Victory	B	645 ^{a,b,c,d,e,f,g}	1371 ^{a,b,c,d,e,f,g,h,i,j}	2017	2.1	457 ^{b,c,d,e,f,g,h,i}	943 ^{a,b,c,d,e,f,g,h,i,j,k}	1400	2.1	865 ^{a,b,c,d,e,f,g}	1830 ^{a,b,c,d,e,f,g,h,}	2695	2.1
Shetland	B	714 ^{a,b,c,d,e,f,g}	1271 ^{a,b,c,d,e,f,g,h,i,j}	1985	1.8	–	–	–	–	918 ^{a,b,c,d,e,f,g}	1367 ^{a,b,c,d,e,f,g,h,i,j}	2285	1.5
Cultra	PR	852 ^{a,b,c,d,e,f,g}	1056 ^{a,b,c,d,e,f,g,h,i,j,k}	1907	1.2	1014 ^{a,b,c,d,e,f}	1192 ^{a,b,c,d,e,f,g,h,i,j}	2206	1.2	625 ^{a,b,c,d,e,f,g}	838 ^{a,b,c,d,e,f,g,h,i,j,k}	1463	1.3
Lumper	B	845 ^{a,b,c,d,e,f,g}	1051 ^{a,b,c,d,e,f,g,h,i,j,k}	1896	1.2	617 ^{a,b,c,d,e,f,g}	751 ^{a,b,c,d,e,f,g,h,i,j,k,l}	1367	1.2	–	–	–	–
Mustang	R	779 ^{a,b,c,d,e,f,g}	1110 ^{a,b,c,d,e,f,g,h,i,j}	1888	1.4	361 ^{d,e,f,g,h,i}	668 ^{a,b,c,d,e,f,g,h,i,j,k,l}	1029	1.8	660 ^{a,b,c,d,e,f,g}	1115 ^{a,b,c,d,e,f,g,h,i,j}	1775	1.7
Saturna	Y	999 ^{a,b,c,d,e,f,g}	884 ^{a,b,c,d,e,f,g,h,i,j,k}	1883	0.9	624 ^{a,b,c,d,e,f,g}	632 ^{a,b,c,d,e,f,g,h,i,j,k,l}	1256	1.0	–	–	–	–
Saxon	Y	672 ^{a,b,c,d,e,f,g}	1210 ^{a,b,c,d,e,f,g,h,i,j}	1882	1.8	463 ^{a,b,c,d,e,f,g,h}	902 ^{a,b,c,d,e,f,g,h,i,j,k}	1365	1.9	–	–	–	–
Victoria	W	788 ^{a,b,c,d,e,f,g}	1062 ^{a,b,c,d,e,f,g,h,i,j,k}	1849	1.3	*1012 ^{a,b,c,d,e,f}	*1189 ^{a,b,c,d,e,f,g,h,i,j}	2201	1.2	–	–	–	–
Setanta	R	820 ^{a,b,c,d,e,f,g}	951 ^{a,b,c,d,e,f,g,h,i,j,k}	1770	1.2	*374 ^{d,e,f,g,h,i}	*441 ^{f,g,h,i,j,k,l,m}	815	1.2	545 ^{a,b,c,d,e,f,g,h}	719 ^{a,b,c,d,e,f,g,h,i,j,k,l}	1263	1.3
Fianna	R	827 ^{a,b,c,d,e,f,g}	930 ^{a,b,c,d,e,f,g,h,i,j,k}	1757	1.1	367 ^{d,e,f,g,h,i}	466 ^{f,g,h,i,j,k,l,m}	833	1.3	951 ^{a,b,c,d,e,f,g}	1100 ^{a,b,c,d,e,f,g,h,i,j}	2051	1.2
Congo	B	903 ^{a,b,c,d,e,f,g}	812 ^{a,b,c,d,e,f,g,h,i,j,k,l}	1715	0.9	1277 ^{a,b,c,d,e}	1006 ^{a,b,c,d,e,f,g,h,i,j,k}	2283	0.8	–	–	–	–
Toluca	PR	546 ^{a,b,c,d,e,f,g,h}	1168 ^{a,b,c,d,e,f,g,h,i,j}	1714	2.1	289 ^{d,e,f,g,h,i}	734 ^{a,b,c,d,e,f,g,h,i,j,k,l}	1023	2.5	796 ^{a,b,c,d,e,f,g}	1744 ^{a,b,c,d,e,f,g,h,i}	2540	2.2
Biogold	W	348 ^{d,e,f,g,h,i}	1240 ^{a,b,c,d,e,f,g,h,i,j}	1587	3.6	*209 ^{e,f,g,h,i,j}	*941 ^{a,b,c,d,e,f,g,h,i,j,k}	1150	4.5	436 ^{b,c,d,e,f,g,h,i}	1554 ^{a,b,c,d,e,f,g,h,i,j}	1990	3.6
Pentland Dell	W	573 ^{a,b,c,d,e,f,g}	952 ^{a,b,c,d,e,f,g,h,i,j,k}	1525	1.7	–	–	–	–	1296 ^{a,b,c,d,e}	2119 ^{a,b,c,d,e,f,g}	3415	1.6
Rooster	R	654 ^{a,b,c,d,e,f,g}	802 ^{a,b,c,d,e,f,g,h,i,j,k,l}	1456	1.2	353 ^{d,e,f,g,h,i}	569 ^{c,d,e,f,g,h,i,j,k,l,m}	922	1.6	750 ^{a,b,c,d,e,f,g}	1113 ^{a,b,c,d,e,f,g,h,i,j}	1864	1.5
Record	Y	619 ^{a,b,c,d,e,f,g}	821 ^{a,b,c,d,e,f,g,h,i,j,k}	1440	1.3	421 ^{c,d,e,f,g,h,i}	751 ^{a,b,c,d,e,f,g,h,i,j,k,l}	1171	1.8	882 ^{a,b,c,d,e,f,g}	1220 ^{a,b,c,d,e,f,g,h,i,j}	2102	1.4
Cara	PR	630 ^{a,b,c,d,e,f,g}	702 ^{a,b,c,d,e,f,g,h,i,j,k,l}	1332	1.1	*493 ^{a,b,c,d,e,f,g,h}	*626 ^{b,c,d,e,f,g,h,i,j,k,l,m}	1118	1.3	935 ^{a,b,c,d,e,f,g}	1145 ^{a,b,c,d,e,f,g,h,i,j}	2080	1.2
Craigs Alliance	Y	417 ^{c,d,e,f,g,h,i}	860 ^{a,b,c,d,e,f,g,h,i,j,k}	1277	2.1	*390 ^{c,d,e,f,g,h,i}	*885 ^{a,b,c,d,e,f,g,h,i,j,k}	1275	2.3	519 ^{a,b,c,d,e,f,g,h}	1178 ^{a,b,c,d,e,f,g,h,i,j}	1696	2.3
Red Cara	R	*614 ^{a,b,c,d,e,f,g}	*656 ^{a,b,c,d,e,f,g,h,i,j,k,l}	1270	1.1	486 ^{a,b,c,d,e,f,g,h}	618 ^{c,d,e,f,g,h,i,j,k,l,m}	1105	1.3	1456 ^{a,b,c,d,e}	1522 ^{a,b,c,d,e,f,g,h,i,j}	2978	1.0
Maris Piper	W	554 ^{a,b,c,d,e,f,g,h}	665 ^{a,b,c,d,e,f,g,h,i,j,k,l}	1219	1.2	*431 ^{b,c,d,e,f,g,h,i}	*696 ^{a,b,c,d,e,f,g,h,i,j,k,l}	1127	1.6	763 ^{a,b,c,d,e,f,g}	1077 ^{a,b,c,d,e,f,g,h,i,j,k}	1840	1.4
Red Pontiac	R	541 ^{a,b,c,d,e,f,g,h}	637 ^{a,b,c,d,e,f,g,h,i,j,k,l}	1178	1.2	398 ^{c,d,e,f,g,h,i}	535 ^{c,d,e,f,g,h,i,j,k,l,m}	933	1.3	746 ^{a,b,c,d,e,f,g}	1001 ^{a,b,c,d,e,f,g,h,i,j,k}	1747	1.3
Shannon	R	397 ^{c,d,e,f,g,h,i}	658 ^{a,b,c,d,e,f,g,h,i,j,k,l}	1055	1.7	*165 ^{e,f,g,h,i,j}	*318 ^{i,j,k,l,m,n}	483	1.9	422 ^{b,c,d,e,f,g,h,i}	806 ^{a,b,c,d,e,f,g,h,i,j,k,l}	1228	1.9
Lady Balfour	PR	333 ^{d,e,f,g,h,i}	427 ^{g,h,i,j,k,l,m}	759	1.3	*436 ^{b,c,d,e,f,g,h,i}	*504 ^{e,f,g,h,i,j,k,l,m}	941	1.2	475 ^{a,b,c,d,e,f,g,h}	669 ^{a,b,c,d,e,f,g,h,i,j,k,l}	1143	1.4
Salad Blue	B	331 ^{d,e,f,g,h,i}	397 ^{h,i,j,k,l,m}	728	1.2	*263 ^{d,e,f,g,h,i}	*403 ^{i,j,k,l,m}	666	1.5	359 ^{d,e,f,g,h,i}	525 ^{d,e,f,g,h,i,j,k,l,m}	884	1.5
Golden Wonder	Y	405 ^{c,d,e,f,g,h,i}	319 ^{i,j,k,l,m,n}	724	0.8	186 ^{e,f,g,h,i,j}	150 ^{k,l,m}	336	0.8	617 ^{a,b,c,d,e,f,g}	542 ^{c,d,e,f,g,h,i,j,k,l,m}	1159	0.9

DW: dry weight. W=white, Y=yellow, P=pink, R=red, B=blue, PR=part red. Means with different letters are significantly different at $p<0.05$ within α-solanine and α-chaconine results. Values reported for the Duleek and Carlow sites are the mean of two (n=2) and three (n=3) field replicates respectively , except for mean values of Carlow marked with *, which are the mean of two replicates. – : no data available

Table 2. α-solanine, α-chaconine, total glycolakaloid content (α-solanine + α-chaconine) and ratio of α-chaconine:α-solanine in the flesh of sixty potato varieties grown at two locations in Ireland over two years. Results expressed as mg kg^{-1} DW.

variety	flesh colour	Carlow 2010				Carlow 2011				Duleek 2010			
		α-solanine (A)	α-chaconine (B)	total (A+B)	ratio (B/A)	α-solanine (A)	α-chaconine (B)	total (A+B)	ratio (B/A)	α-solanine (A)	α-chaconine (B)	total (A+B)	ratio (B/A)
International Kidney	LY	580^{a}	377^{a}	957	0.7	118^{a,b,c,d,e}	48^{b,c,d,e,f,g,h,i,j,k,l,m,n,o,p}	166	0.4	225^{a,b,c,d}	139^{a,b,c,d,e,f,g,h}	364	0.6
Craigs Royal	Y	478^{a,b}	356^{a}	834	0.7	63^{b,c,d,e,f,g}	36^{e,f,g,h,i,j,k,l,m,n,o,p,q,r}	98	0.6	258^{a,b,c}	151^{a,b,c,d,e,f,g}	409	0.6
May Queen	C	334^{a,b,c}	349^{a}	683	1.0	28^{d,e,f,g,h,i}	34^{e,f,g,h,i,j,k,l,m,n,o,p,q,r}	62	1.2	48^{b,c,d,e,f,g}	62^{b,c,d,e,f,g,h,i,j,k,l,m,n,o,p}	110	1.3
Arran Chief	W	294^{a,b,c}	305^{a,b}	599	1.0	*86^{a,b,c,d,e}	*52^{b,c,d,e,f,g,h,i,j,k,l,m,n,o,p}	138	0.6	137^{a,b,c,d}	116^{a,b,c,d,e,f,g,h,i,j,k,l}	253	0.8
Druid	LY	299^{a,b,c}	263^{a,b}	563	0.9	158^{a,b,c,d}	109^{a,b,c,d,e,f,g,h,i,j,k,l,m}	267	0.7	266^{a,b,c}	209^{a,b,c}	474	0.8
Russett Burbank	C	*329^{a,b,c}	*161^{a,b,c,d,e}	490	0.5	34^{c,d,e,f,g,h}	20^{k,l,m,n,o,p,q,r}	54	0.6	251^{a,b,c}	173^{a,b,c,d,e}	424	0.7
Pentland Ivory	LY	291^{a,b,c}	176^{a,b,c,d}	467	0.6	188^{a,b,c,d}	*66^{a,b,c,d,e,f,g,h,i,j,k,l,m,n}	254	0.4	229^{a,b,c}	117^{a,b,c,d,e,f,g,h,i,j,k}	346	0.5
Lewis black	PB-C	199^{a,b,c,d}	147^{a,b,c,d,e,f,g,h}	345	0.7	–	–	–	–	35^{c,d,e,f,g,h}	36^{e,f,g,h,i,j,k,l,m,n,o,p,q,r}	71	1.0
Arran Pilot	C	151^{a,b,c,d}	185^{a,b,c}	337	1.2	*66^{a,b,c,d,e,f}	*70^{a,b,c,d,e,f,g,h,i,j,k,l,m}	136	1.1	68^{a,b,c,d,e,f}	80^{a,b,c,d,e,f,g,h,i,j,k,l,m}	147	1.2
Lady Rosetta	LY	*197^{a,b,c,d}	*105^{a,b,c,d,e,f,g,h,i,j,k,l,m}	302	0.5	27^{d,e,f,g,h,i}	21^{k,l,m,n,o,p,q,r}	48	0.8	68^{a,b,c,d,e,f}	53^{b,c,d,e,f,g,h,i,j,k,l,m,n,o,p}	120	0.8
Beauty of Hebron	LY	180^{a,b,c,d}	95^{a,b,c,d,e,f,g,h,i,j,k,l,m}	274	0.5	*87^{a,b,c,d,e}	*38^{d,e,f,g,h,i,j,k,l,m,n,o,p,q,r}	124	0.4	439^{a,b,c}	137^{a,b,c,d,e,f,g,h,i}	577	0.3
Axona	C	121^{a,b,c,d}	125^{a,b,c,d,e,f,g,h,i,j,k}	245	1.0	62^{b,c,d,e,f,g}	41^{c,d,e,f,g,h,i,j,k,l,m,n,o,p,q,r}	103	0.7	212^{a,b,c,d}	134^{a,b,c,d,e,f,g,h,i,j}	345	0.6
Duke of York	C	116^{a,b,c,d,e}	127^{a,b,c,d,e,f,g,h,i,j}	244	1.1	49^{b,c,d,e,f,g}	31^{f,g,h,i,j,k,l,m,n,o,p,q,r}	80	0.6	63^{b,c,d,e,f,g}	50^{b,c,d,e,f,g,h,i,j,k,l,m,n,o,p}	114	0.8
Setanta	LY	110^{a,b,c,d,e}	124^{a,b,c,d,e,f,g,h,i,j,k}	234	1.1	*18^{d,e,f,g,h,i}	*9^{o,p,q,r}	27	0.5	55^{b,c,d,e,f,g}	59^{b,c,d,e,f,g,h,i,j,k,l,m,n,o,p}	114	1.1
British Queen	W	129^{a,b,c,d}	95^{a,b,c,d,e,f,g,h,i,j,k,l,m}	224	0.7	*66^{a,b,c,d,e,f}	*28^{g,h,i,j,k,l,m,n,o,p,q,r}	93	0.4	–	–	–	–
Pimpernell	Y	95^{a,b,c,d,e}	126^{a,b,c,d,e,f,g,h,i,j}	221	1.3	64^{a,b,c,d,e,f}	54^{b,c,d,e,f,g,h,i,j,k,l,m,n,o,p}	118	0.8	–	–	–	–
Home Guard	C	111^{a,b,c,d,e}	109^{a,b,c,d,e,f,g,h,i,j,k,l}	221	1.0	*86^{a,b,c,d,e}	*61^{b,c,d,e,f,g,h,i,j,k,l,m,n,o,p}	147	0.7	153^{a,b,c,d}	125^{a,b,c,d,e,f,g,h,i,j,k}	278	0.8
Edgecote purple	C	*105^{a,b,c,d,e}	*103^{a,b,c,d,e,f,g,h,i,j,k,l,m}	207	1.0	*43^{c,d,e,f,g}	*28^{g,h,i,j,k,l,m,n,o,p,q,r}	71	0.7	197^{a,b,c,d}	147^{a,b,c,d,e,f,g,h}	344	0.7
Shetland	W	90^{a,b,c,d,e}	111^{a,b,c,d,e,f,g,h,i,j,k,l}	202	1.2	–	–	–	–	310^{a,b,c}	263^{a,b}	573	0.8
Edzell Blue	C	111^{a,b,c,d,e}	90^{a,b,c,d,e,f,g,h,i,j,k,l,m}	201	0.8	71^{a,b,c,d,e,f}	31^{f,g,h,i,j,k,l,m,n,o,p,q,r}	102	0.4	94^{a,b,c,d,e}	61^{b,c,d,e,f,g,h,i,j,k,l,m,n,o,p}	156	0.6
Sharpes Express	C	112^{a,b,c,d,e}	78^{b,c,d,e,f,g,h,i,j,k,l,m}	190	0.7	32^{c,d,e,f,g,h}	21^{k,l,m,n,o,p,q,r}	52	0.6	78^{a,b,c,d,e,f}	54^{b,c,d,e,f,g,h,i,j,k,l,m,n,o,p}	132	0.7
Burren	Y	91^{a,b,c,d,e}	93^{a,b,c,d,e,f,g,h,i,j,k,l,m}	183	1.0	13^{e,f,g,h,i}	12^{o,p,q,r}	25	0.9	21^{d,e,f,g,h,i}	23^{k,l,m,n,o,p,q,r}	44	1.1
Nicola	LY	80^{a,b,c,d,e,f}	83^{a,b,c,d,e,f,g,h,i,j,k,l,m}	163	1.0	28^{d,e,f,g,h,i}	23^{k,l,m,n,o,p,q,r}	51	0.8	38^{c,d,e,f,g}	29^{f,g,h,i,j,k,l,m,n,o,p,q,r}	67	0.8
Congo	B	105^{a,b,c,d,e}	55^{b,c,d,e,f,g,h,i,j,k,l,m,n,o,p}	159	0.5	265^{a,b,c}	147^{a,b,c,d,e,f,g}	412	0.6	–	–	–	–
Record	Y	83^{a,b,c,d,e}	74^{a,b,c,d,e,f,g,h,i,j,k,l,m}	157	0.9	17^{d,e,f,g,h,i}	15^{l,m,n,o,p,q,r}	33	0.9	25^{d,e,f,g,h,i}	24^{j,k,l,m,n,o,p,q,r}	50	1.0
Mustang	Y	77^{a,b,c,d,e,f}	68^{a,b,c,d,e,f,g,h,i,j,k,l,m}	145	0.9	7^{g,h,i}	10^{o,p,q,r}	17	1.4	46^{c,d,e,f,g}	62^{b,c,d,e,f,g,h,i,j,k,l,m,n,o,p}	108	1.3
Pink Fir Apple	C	74^{a,b,c,d,e,f}	66^{a,b,c,d,e,f,g,h,i,j,k,l,m}	141	0.9	42^{c,d,e,f,g}	32^{f,g,h,i,j,k,l,m,n,o,p,q,r}	73	0.8	41^{c,d,e,f,g}	32^{e,f,g,h,i,j,k,l,m,n,o,p,q,r}	74	0.8
Golden Wonder	C	90^{a,b,c,d,e}	48^{b,c,d,e,f,g,h,i,j,k,l,m,n,o,p}	138	0.5	11^{e,f,g,h,i}	6^{r}	17	0.5	23^{d,e,f,g,h,i}	18^{k,l,m,n,o,p,q,r}	41	0.8
Flourball	C	*74^{a,b,c,d,e,f}	*58^{b,c,d,e,f,g,h,i,j,k,l,m,n,o,p}	131	0.8	26^{d,e,f,g,h,i}	15^{l,m,n,o,p,q,r}	41	0.6	39^{c,d,e,f,g}	34^{e,f,g,h,i,j,k,l,m,n,o,p,q,r}	73	0.9
Kerrs Pink	LY	59^{b,c,d,e,f,g}	72^{a,b,c,d,e,f,g,h,i,j,k,l,m}	130	1.2	–	–	–	–	125^{a,b,c,d}	110^{a,b,c,d,e,f,g,h,i,j,k,l}	235	0.9

(continued)

Table 2 - Continued.

variety	skin colour	Carlow 2010 α-solanine (A)	α-chaconine (B)	total (A+B)	ratio (B/A)	Carlow 2011 α-solanine (A)	α-chaconine (B)	total (A+B)	ratio (B/A)	Duleek 2010 α-solanine (A)	α-chaconine (B)	total (A+B)	ratio (B/A)
Pentland Dell	C	58 b,c,d,e,f,g	71 a,b,c,d,e,f,g,h,i,j,k,l,m	129	1.2	–	–	–	–	291 a,b,c	198 a,b,c	489	0.7
Ulster Sceptre	C	72 a,b,c,d,e,f	53 b,c,d,e,f,g,h,i,j,k,l,m,n,o,p	125	0.7	44 c,d,e,f,g	27 h,i,j,k,l,m,n,o,p,q,r	71	0.6	70 a,b,c,d,e,f	42 c,d,e,f,g,h,i,j,k,l,m,n,o,p,q,r	112	0.6
Craigs Alliance	LY	61 b,c,d,e,f,g	62 b,c,d,e,f,g,h,i,j,k,l,m,n,o,p	123	1.0	*27 d,e,f,g,h,i	*20 k,l,m,n,o,p,q,r	47	0.8	77 a,b,c,d,e,f	51 b,c,d,e,f,g,h,i,j,k,l,m,n,o,p	128	0.7
Eersterling	C	66 a,b,c,d,e,f	50 b,c,d,e,f,g,h,i,j,k,l,m,n,o,p	116	0.8	22 d,e,f,g,h,i	17 k,l,m,n,o,p,q,r	39	0.8	69 a,b,c,d,e,f	71 a,b,c,d,e,f,g,h,i,j,k,l,m	140	1.0
Lady Claire	LY	52 b,c,d,e,f,g	57 b,c,d,e,f,g,h,i,j,k,l,m,n,o,p	109	1.1	63 b,c,d,e,f,g	43 c,d,e,f,g,h,i,j,k,l,m,n,o,p,q,r	106	0.7	232 a,b,c	156 a,b,c,d,e,f	389	0.7
Victoria	C	53 b,c,d,e,f,g	55 b,c,d,e,f,g,h,i,j,k,l,m,n,o,p	109	1.0	*16 d,e,f,g,h,i	*12 n,o,p,q,r	28	0.8	–	–	–	–
Salad Blue	B	62 b,c,d,e,f,g	42 c,d,e,f,g,h,i,j,k,l,m,n,o,p,q	104	0.7	*57 b,c,d,e,f,g	*36 e,f,g,h,i,j,k,l,m,n,o,p,q,r	93	0.6	71 a,b,c,d,e,f	40 c,d,e,f,g,h,i,j,k,l,m,n,o,p,q,r	112	0.6
Saturna	LY	41 c,d,e,f,g	54 b,c,d,e,f,g,h,i,j,k,l,m,n,o,p	95	1.3	72 a,b,c,d,e,f	36 e,f,g,h,i,j,k,l,m,n,o,p,q,r	108	0.5	–	–	–	–
Collen	LY	45 c,d,e,f,g	37 e,f,g,h,i,j,k,l,m,n,o,p,q	82	0.8	53 b,c,d,e,f,g	26 i,j,k,l,m,n,o,p,q,r	79	0.5	47 b,c,d,e,f,g	27 h,i,j,k,l,m,n,o,p,q,r	74	0.6
Toluca	LY	31 c,d,e,f,g,h	51 b,c,d,e,f,g,h,i,j,k,l,m,n,o,p	82	1.6	34 c,d,e,f,g,h	31 f,g,h,i,j,k,l,m,n,o,p,q,r	64	0.9	60 b,c,d,e,f,g	75 a,b,c,d,e,f,g,h,i,j,k,l,m	135	1.3
King Edward	C	39 c,d,e,f,g	40 d,e,f,g,h,i,j,k,l,m,n,o,p,q	78	1.0	*12 e,f,g,h,i	*8 p,q,r	20	0.7	10 e,f,g,h,i	16 k,l,m,n,o,p,q,r	27	1.6
Arran Victory	C	30 c,d,e,f,g,h	46 b,c,d,e,f,g,h,i,j,k,l,m,n,o,p,q	76	1.5	18 d,e,f,g,h,i	22 k,l,m,n,o,p,q,r	40	1.3	–	–	–	–
Ambo	C	32 c,d,e,f,g,h	42 c,d,e,f,g,h,i,j,k,l,m,n,o,p,q	74	1.3	22 d,e,f,g,h,i	17 k,l,m,n,o,p,q,r	38	0.8	12 e,f,g,h,i	17 k,l,m,n,o,p,q,r	29	1.4
Fianna	C	34 c,d,e,f,g,h	40 d,e,f,g,h,i,j,k,l,m,n,o,p,q	74	1.2	20 d,e,f,g,h,i	*14 m,n,o,p,q,r	34	0.7	50 b,c,d,e,f,g	43 c,d,e,f,g,h,i,j,k,l,m,n,o,p,q,r	93	0.9
Lady Balfour	W	35 c,d,e,f,g	35 e,f,g,h,i,j,k,l,m,n,o,p,q	70	1.0	–	–	–	–	27 d,e,f,g,h,i	19 k,l,m,n,o,p,q,r	46	0.7
Red Pontiac	W	35 c,d,e,f,g	33 e,f,g,h,i,j,k,l,m,n,o,p,q	68	0.9	15 d,e,f,g,h,i	12 o,p,q,r	27	0.8	27 d,e,f,g,h,i	22 k,l,m,n,o,p,q,r	49	0.8
Shannon	LY	31 c,d,e,f,g,h	32 f,g,h,i,j,k,l,m,n,o,p,q	63	1.0	*16 d,e,f,g,h,i	*12 o,p,q,r	27	0.7	42 c,d,e,f,g	42 c,d,e,f,g,h,i,j,k,l,m,n,o,p,q,r	83	1.0
Rooster	Y	29 c,d,e,f,g,h,i	26 i,j,k,l,m,n,o,p,q	55	0.9	*7 f,g,h,i	*6 q,r	14	0.8	10 e,f,g,h,i	12 o,p,q,r	21	1.2
Cara	C	24 d,e,f,g,h,i	26 i,j,k,l,m,n,o,p,q	50	1.1	*17 d,e,f,g,h,i	*12 n,o,p,q,r	29	0.7	54 b,c,d,e,f,g	54 b,c,d,e,f,g,h,i,j,k,l,m,n,o,p	108	1.0
Harlequin	C	25 d,e,f,g,h,i	24 k,l,m,n,o,p,q	48	1.0	30 c,d,e,f,g,h	21 k,l,m,n,o,p,q,r	51	0.7	39 c,d,e,f,g	37 d,e,f,g,h,i,j,k,l,m,n,o,p,q,r	77	1.0
Red Cara	Y	*18 d,e,f,g,h,i	*22 k,l,m,n,o,p,q	41	1.2	15 e,f,g,h,i	14 m,n,o,p,q,r	29	1.0	56 b,c,d,e,f,g	52 b,c,d,e,f,g,h,i,j,k,l,m,n,o,p	108	0.9
Maris Piper	C	18 d,e,f,g,h,i	20 k,l,m,n,o,p,q	38	1.2	*23 d,e,f,g,h,i	*18 k,l,m,n,o,p,q,r	41	0.8	59 b,c,d,e,f,g	58 b,c,d,e,f,g,h,i,j,k,l,m,n,o,p	117	1.0
Sarpo Mira	LY	20 d,e,f,g,h,i	18 k,l,m,n,o,p,q	38	0.9	5 i	5 r	10	0.9	–	–	–	–
Bionica	C	18 d,e,f,g,h,i	19 k,l,m,n,o,p,q	37	1.0	*7 f,g,h,i	*4 r	12	0.6	8 e,f,g,h,i	8 p,q,r	16	0.9
Saxon	LY	16 d,e,f,g,h,i	21 k,l,m,n,o,p,q	37	1.4	–	–	–	–	–	–	–	–
Charlotte	LY	15 d,e,f,g,h,i	17 k,l,m,n,o,p,q	32	1.1	27 d,e,f,g,h,i	16 k,l,m,n,o,p,q,r	44	0.6	29 c,d,e,f,g,h,i	25 i,j,k,l,m,n,o,p,q,r	54	0.9
Lumper	PB-C	16 d,e,f,g,h,i	15 l,m,n,o,p,q	31	0.9	17 d,e,f,g,h,i	8 q,r	25	0.5	–	–	–	–
Early Rose	LY	12 e,f,g,h,i	16 l,m,n,o,p,q	29	1.3	17 d,e,f,g,h,i	16 l,m,n,o,p,q,r	33	1.0	27 d,e,f,g,h,i	36 e,f,g,h,i,j,k,l,m,n,o,p,q,r	63	1.3
Biogold	LY	5 i	8 q,r	13	1.5	*ND	*4 r	4	–	4 i	14 m,n,o,p,q,r	18	3.1
Cultra	C	5 h,i	5 r	10	0.9	10 e,f,g,h,i	7 q,r	17	0.7	18 d,e,f,g,h,i	19 k,l,m,n,o,p,q,r	37	1.1

DW: dry weight. W=white, C=cream, LY=light yellow, Y=yellow, B=blue, PB-C=part blue, cream. Means with different letters are significantly different at $p<0.05$. Values reported for the Duleek and Carlow sites are the mean of two (n=2) and three (n=3) field replicates respectively, except for mean values of Carlow marked with *, which are the mean of two replicates. – : no data available

The values reported in the current work are in line with others found in the literature. Previous studies also encountered considerable variation among varieties, reporting total glycoalkaloid contents of 84 to 2226 mg kg^{-1} in dry peel and 5 to 592 mg kg^{-1} in dry flesh (Friedman and others 2003), 174 to 5497 mg kg^{-1} in dry peel and up to 642 mg kg^{-1} in dry boiled flesh (Sotelo and Serrano 2000), or 585 to 5342 mg kg^{-1} in dry peel and from 7 to 466 mg kg^{-1} in dry flesh (Deußer and others 2012) .

The α-chaconine and α-solanine quantities found in tubers showed a strong positive correlation, with Pearson's coefficients of 0.869 and 0.923 in skin and flesh tissues respectively at $p<0.0001$. Analysis of variance (ANOVA) showed a significant difference at $p<0.05$ between tissues, with mean ratio values across years and sites of 1.4 and 0.9 in skin and flesh respectively. This suggests that both glycoalkaloids are accumulated in a coordinated manner, with, in general, the skin of tubers tending to accumulate more α-chaconine than the flesh. Since α-chaconine is more toxic than α-solanine, it can be assumed that the skin of potatoes is not only more toxic than the flesh due to the glycoalkaloid levels but also because of the glycoalkaloid profile. However, it cannot be concluded that this is true in every case; lower quantities of α-chaconine than α-solanine were found in the skin of 7 out of the 60 varieties analyzed, with higher quantities of α-chaconine than α-solanine also found in the flesh in 4 to 30 varieties depending on the site and year of cultivation. The genotype affects the proportion of both glycoalkaloids in tubers, but it is also affected by environment. ANOVA showed that year of cultivation and variety were significant effects ($p<0.05$). The α-chaconine to α-solanine ratio in the skin ranged from 0.7 to 4.5 and from 0.3 to 3.1 in the flesh.

Previous studies generally report higher α-chaconine to α-solanine ratios in the skin than in the flesh, but with most finding ratios higher than 1. A study including 8 potato cultivars found ratios higher than 1 for all varieties regardless of tissue type, albeit with generally higher ratios in the skin than in the flesh (Friedman and others 2003). Another study in 12 commercial varieties reported that α-chaconine accounts for between 65 and 75% of the total glycoalkaloids in the peel of tubers, equivalent to a ratio of 1.8 to 2.4, with irregular ratios, higher and lower than 1, in boiled flesh (Sotelo and Serrano 2000). Ratios from 0.83 to 2.38 in the flesh and from 1.05 to 3.35 in the peel were found in 17 varieties of potato (Deußer and others 2012). Other studies report ratios ranging from 0.03 to 15.42 in the flesh and from 0.007 to 54.03 in the skin (Aziz and others 2012), or ratios of 0.2 and 0.17 for skin and flesh respectively (Wu and others 2012).

The commonly accepted limit for glycoalkaloids in whole commercial potatoes is 200 mg kg^{-1} of fresh weight (Smith and others 1996), equivalent to roughly 1000 mg kg^{-1} of DW if we assume a water content of 80%. With a few exceptions, the total glycoalkaloid content in the skin of tubers was above 1000 mg kg^{-1} DW, while in the flesh, none of the varieties studied were over this limit, with the highest value of 957 mg kg^{-1} DW found in variety 'International Kidney' grown in Carlow in 2010. If we assume this limit to be adequate, then the consumption of peeled tubers of any variety included in this study can be considered safe. Nevertheless, some varieties could go over this limit if the skin is not removed. It has been reported that the skin of tubers represents between 7 to 11% of total tuber weight (Friedman and others 2003). Applying the upper 11% value to the results reported here, whole tuber contents would be higher than the safe limit for variety 'Beauty of Hebron' grown in 2010 in Carlow and Duleek and varieties 'May Queen', 'Craigs Royal' and 'International Kidney' grown in Carlow in 2010. Heritage varieties 'Beauty of Hebron' and 'International Kidney' are suitable to be eaten unpeeled in salads, so depending on cultivation and storage conditions, they might be potentially well above the recommended threshold for glycoalkaloids. ‘Beauty of Hebron’ is not currently in commercial production and its consumption therefore extremely limited, but ‘International Kidney’, also known as ‘Jersey Royals’, is a commercial cultivar and could therefore be problematic.

In Ireland, the daily potato consumption is 158 g per capita (Sector profile - Potatoes 2001) and variety ‘Rooster’ accounts for 59% of potatoes purchased (Bourke 2012). The daily intake of total glycoalkaloids could be between 0.4 and 1.7 mg per person per day if the data reported in this study for the flesh of ‘Rooster’ is considered. If we assume that potatoes are eaten with the skin, and applying the 11% of peel in relation to whole tuber, the daily intake per person of total glycoalkaloids would be between 3.6 and 8 mg. The toxic dose in humans has been calculated to be 2-5 mg of glycoalkaloids per kg of body weight, so it appears that Irish consumers are far from reaching toxic doses. Nevertheless, chronic effects are largely unknown, as well as interactions between α-solanine and α-chaconine and with other food constituents that could potentiate or diminish their toxic effects (Friedman 2006).

Despite the status of glycoalkaloids as potentially dangerous components of potatoes, they could also prove beneficial. The potato industry produces large quantities of potato peel waste and its disposal represents a problem. Certain components of potato peels, such as phenolic compounds, dietary fibre and also glycoalkaloids, could potentially be used as raw materials by other industries. Solanidine can be released from α-solanine and α-chaconine by enzymatic or acid hydrolysis and is a promising intermediate in the synthesis of steroid hormones (Schieber and Saldaña 2009). The potato varieties ‘Lady Rosetta’, ‘Lady Claire’ and ‘Saturna’ are used for the chip-processing industry and varieties ‘Maris Piper’, ‘Pentland Dell’ and ‘King Edward’ to manufacture French fries. These six varieties are included in the present work, with variety ‘Lady Claire’ showing the highest mean content of glycoalkaloids in the skin.

Table 3. ANOVA p-values at 95% confidence interval for main effects and interactions.

effect	total glycoalkaloids
site	0.1152
year	<0.0001
variety	<0.0001
tissue	<0.0001
replicate(site)	0.3341
replicate(year)	0.063
site*variety	<0.0001
site*tissue	0.0035
year*variety	<0.0001
year*tissue	<0.0001
variety*tissue	<0.0001

N/A: not applicable

The site of cultivation had no significant effect on the content of total glycoalkaloids (Table 3). However there was a significant difference between 2010 and 2011 in Carlow, with tubers accumulating on average twice as much total glycoalkaloids the first year of cultivation than the second. Curiously, there were significant interactions between site of cultivation and variety and between year of cultivation and variety, which mean that the action and extent of the environmental effects are different depending on the variety. Figure 2 shows the climatic conditions for both years, with 2010 being on average slightly warmer and with little difference in rainfall or solar radiation. However, extreme temperature data show larger differences for 2010 than for 2011, which may partially explain the differences observed. Responses of glycoalkaloid levels in tubers to environmental effects seem to be variable depending on the variety, with some varieties showing differences in stressed conditions while others do not seem to be affected (Papathanasiou and others 1999; Bejarano and others 2000). Studies in controlled growing environments have found that heat stress increase the glycoalkaloid content, with diverse results reported

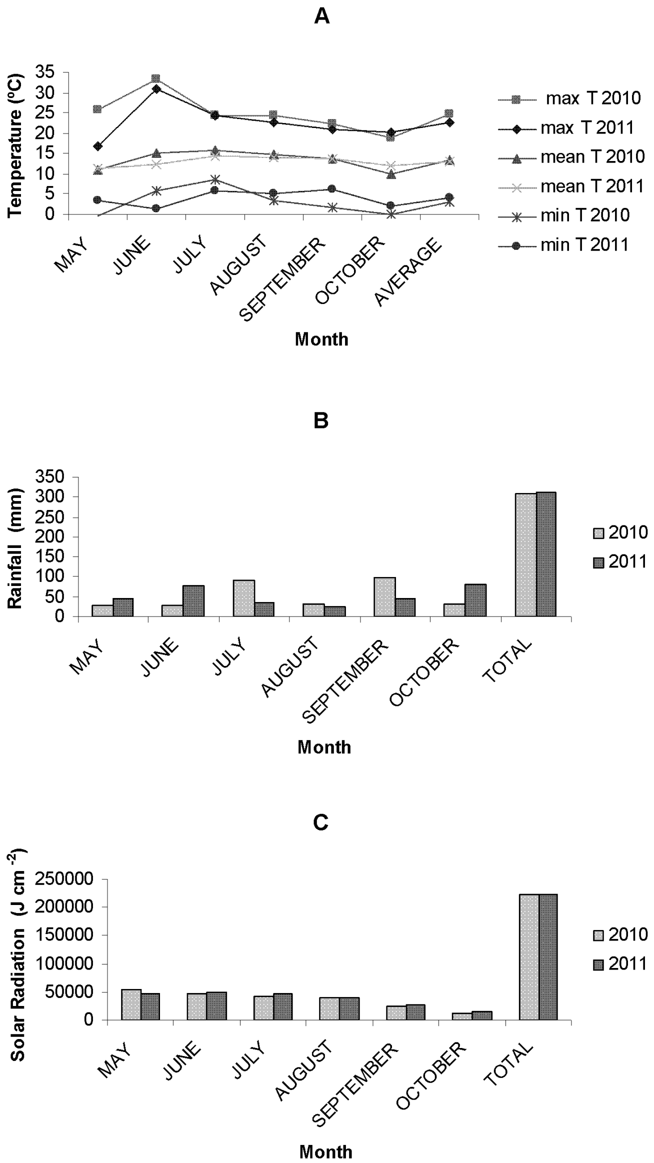

Figure 2. Climatic conditions at Carlow trial site over two years. A) Minima, maxima and mean temperatures; B) Monthly and total rainfall; C) Monthly and total solar radiation.

for low temperatures (Nitithamyong and others 1999; Papathanasiou and others 1999). Drought stress seems to increase the glycoalkaloid content as well, but excess of water has the same effect at low temperatures during later stages of development only

(Papathanasiou and others 1999; Bejarano and others 2000). A study looking at 3 varieties planted in 4 sites over 3 years found only one of the sites and one of the years significantly different from the rest (Haase 2010). The authors attribute the difference between sites to soil characteristics, associating loamy soil with higher levels of glycoalkaloids. Soil texture analysis showed a more sandy soil in Duleek than in Carlow, with contents of silt and clay of 5.8% and 13.8% respectively, however we did not find a significant difference between both sites. Cold and wet periods during summer were also associated with higher levels of glycoalkaloids.

The values reported in this study are for uncooked potatoes analyzed after harvest. Any use of these data in relation to dietary intake must consider the effect that different processing and storage methods may have on the levels of glycoalkaloids and further studies to address this would be of interest.

CONCLUSION

Glycoalkaloid content in skin and flesh tissues was investigated in a large number of varieties of potato, which could be of interest to potato breeders, the potato industry, policymakers and the general public. The flesh of all varieties showed lower glycoalkaloid content than the limit commonly accepted as safe. Variety ‘Rooster’ in particular, which is the potato variety most consumed in Ireland, had remarkably low contents. The values reported in this study are for uncooked potatoes analyzed after harvest. Any use of these data in relation to dietary intake must consider the effect that different processing and storage methods may have on the levels of glycoalkaloids.

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