Effect of Light Exposure on the Glycoalkaloid Content of *Solanum phureja* Tubers

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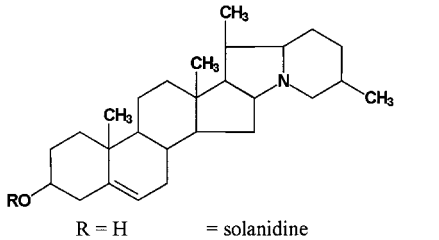
The individual glycoalkaloid contents of tubers from eleven *Solanum phureja* genotypes have been determined prior to and following exposure to light. In all genotypes, light exposure resulted in a statistically significant increase in total glycoalkaloid content. In nine of the genotypes studied, this was not only due to an increase in the levels of the solanidine-based glycoalkaloids, α-solanine and α-chaconine, but also due to the light-induced synthesis of a tomatidenol-based glycoalkaloid, α-solamarine. Those genotypes that accumulated α-solamarine in their tubers also contained tomatidenol-based glycoalkaloids in their leaves, but only solanidine-based glycoalkaloids were detected in the sprouts.

Keywords: *Glycoalkaloids; α-solanine; α-chaconine; α-solamarine; light; tubers; leaves; sprouts*

INTRODUCTION

The steroidal glycoalkaloids are a toxic group of secondary plant compounds commonly found in foliage and tubers of both domesticated and wild species of the Solanaceae (*1, 2*). In the domesticated potato (*Solanum tuberosum* L.), their presence at low concentrations may contribute to the flavor characteristics of processed potato, but at levels above 15 mg per 100 g fresh weight a bitter taste may be detected (*3*). The consumption of large amounts of glycoalkaloids by humans can, however, result in toxic symptoms ranging in severity from nausea to, in extreme cases, death (*4*). In the wild *Solanum* species, frequently used by breeders to introduce desirable attributes to the domesticated potato, the most common glycoalkaloids are α-solanine and α-chaconine (Figure 1), both of which are differently glycosylated forms of the aglycon solanidine and are also the major glycoalkaloids detected in the tubers of the domesticated potato. However, a number of glycoalkaloids containing other aglycons, such as solasodine, tomatidenol, demissidine, and tomatidine (Figure 1), have also been identified, and in some accessions of the wild species may be the predominant tuber glycoalkaloids (*1, 2*).

S. phureja is grown as a cultivated potato species in South America and is a close relative of *S. stenotomum*, which is regarded as an ancestor of the domesticated European potato (*S. tuberosum*) (*5*). *S. phureja* has been utilized as a bridging species to facilitate the transfer of desirable characteristics into the domesticated potato from otherwise incompatible wild species, such as the introduction of late-blight resistance from *S. bulbocastanum* (*6*). Considerable interest is currently being shown in developing *S. phureja* as a crop adapted for European conditions (*7*). Comparatively few investigations have been carried out examining the glycoalkaloid content of *S. phureja* although it has been reported in two independent studies that only solanidine-based glycoalkaloids could be detected in the tubers (*2, 8*).



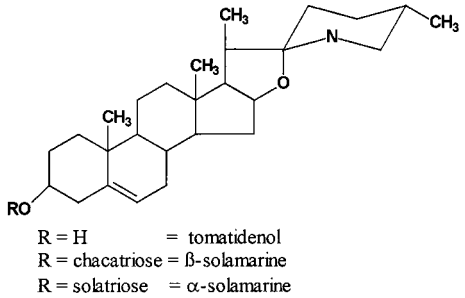


Figure 1. Structures of solanidine- and tomatidenol-based glycoalkaloids.

The concentration of glycoalkaloids in the tubers of the domesticated potato can be significantly increased by post-harvest stress. In particular, exposure to direct sunlight (*9*) or artificial lighting (*10*) can significantly increase the content of α-solanine and α-chaconine, with the magnitude of the observed increases being dependent on both cultivar (*11*) and post-harvest storage conditions (*12*). A recent study of tubers from two long-day adapted *S. phureja* genotypes has revealed that exposure to artificial light resulted not only in a significant increase in α-solanine and α-chaconine content, but also induced the synthesis of an additional tomatidenol-based glycoalkaloid, α-solamarine (Figure 1). This glycoalkaloid was not detected in the tubers prior to light exposure (*13*).

The objective of this study was to determine whether genetic variation could be found within a collection of long-day adapted population of *S. phureja* genotypes for

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Table 1. Mean Tuber Weight per Replicate and the Dry Matter Content (%FDM) of the 11 *Solanum Phureja* Genotypes Utilized in This Study

genotype identity code	abbrev. code	tuber wt (g)[a] set A[b]	tuber wt (g)[a] set B[c]	dry matter[a] (%FDM)[d]
84 1 T8 ExMS 86 (1)	841/01	116	122	21.6
84 1 T8 ExMS 86 (13)	841/13	109	107	20.2
84 1 T24 Ex MS 86 (5)	841/05	105	120	22.4
85 2 T1 ExMS 86 (10)	852/10	105	102	23.0
DB 257/28	DB 257	121	115	20.4
DB 299/14	DB 299	139	147	22.3
DB 300/29	DB 300	102	99	20.6
DB 323/03	DB 323	106	107	23.8
DB 333/16	DB 333	119	123	19.6
DB 337/37	DB 337	91	96	20.6
DB 358/23	DB 358	112	125	22.3
Lsd ($P < 0.05$)[e]		10.1		0.83

[a] All values are means of a single analysis from each of four replicates. [b] Set A = Replicates used for the determination of glycoalkaloid content at commencement of light exposure experiment. [c] Set B = Replicates used for determining effect of light on glycoalkaloid content. [d] FDM = freeze-dried matter. [e] Lsd = Least significant difference.

the photoinduced synthesis of α-solamarine and the other commonly found solanidine-based glycoalkaloids.

MATERIALS AND METHODS

Plant Material. The genotypes utilized in this study were selected from a long-day adapted population of *S. phureja* originally derived from the Commonwealth Potato Collection based and maintained at the Scottish Crop Research Institute, Dundee, UK. Tubers from the 11 genotypes of *S. phureja* (Table 1) were harvested from field plots where they had been grown, using normal agronomic practices, at a trial site located at Mylnefield, Dundee, UK. The tubers from each genotype were harvested two weeks following foliage burn-down, manually washed, and sorted into eight replicates, each of which consisted of five average-sized tubers, the mean tuber weights of which are given in Table 1. These, together with any remaining tubers, were maintained at ambient store temperature (ca. 8 °C) for two weeks and then transferred to a 10 °C store at 85−95% relative humidity. After six weeks of storage, four replicates from each genotype were sampled for subsequent glycoalkaloid analysis. The tubers were cut into eighths, and two opposite eighths were collected and bulked by replicate. These were manually diced and immediately frozen by immersion in liquid nitrogen. After the samples were freeze-dried, they were ground in a mill fitted with a 0.5-mm sieve, and stored at −20 °C until analyzed. The remaining four replicates were utilized in the light-exposure experiment which commenced on the same day as the initial sampling.

Two replicate samples of leaf material were taken from each genotype 8 weeks following sowing. Each replicate was prepared by removing a single stem from 10 plants selected at random from the field-grown plots. The leaves from the top third of each stem were manually removed, bulked by replicate, and immediately frozen by immersion in liquid nitrogen. The frozen samples were freeze-dried, then ground in a mill fitted with a 0.5-mm sieve, and subsequently stored at −20 °C until analyzed.

A bulked sample of potato sprouts from each genotype was prepared by harvesting the sprouts from approximately 12 tubers which had been stored in the dark at 10 °C for 15 weeks. The sprouts, which had an average length of 2−3 cm, were separated from the tubers, immediately frozen in liquid nitrogen, freeze-dried, and milled through a 0.5-mm sieve. The samples were stored at −20 °C, and each sample was subsequently analyzed in duplicate.

Light Exposure. The methodology used to determine the effect of light on tuber glycoalkaloid content was similar to that previously described for *S. tuberosum* (*10*−*12*, *14*). The tubers, once removed from storage, were cut in half longitudinally, and one half was placed, cut-surface down, on a tray lined with absorbant paper. The trays were then placed in a controlled environment chamber set to 20 °C and ambient humidity (ca. 85−95% relative humidity). The tubers were illuminated by high-pressure sodium lights (predominant wavelength 550−650 nm) distributed such as to give a uniform flux density of 140 μmol/m^2/s at tray level. The absorbant paper lining the trays was watered twice daily to prevent any drying-out of the tubers during their period of illumination. The remaining half tubers were placed on identical trays which were inserted into black polyethylene light-proof bags and transferred into the illuminated controlled environmental chamber to serve as nonilluminated dark controls. After 96 h, the illuminated and nonilluminated sets of samples were removed from the environmental chamber, and a 2-mm slice was removed from the cut surface of each halved tuber. The half tubers were then cut into quarters, and two opposite quarters from each tuber were bulked by replicate. These were then diced, frozen in liquid nitrogen, freeze-dried, milled, and stored at −20 °C.

Chemical Analysis. Dry matter content was determined on the basis of the difference in weight before and after freeze-drying, and was expressed in terms of g of freeze-dried matter per 100 g of fresh weight (gFDM/100gFWt).

The glycoalkaloids from the freeze-dried tuber and sprout samples were both extracted using 2% aqueous acetic acid containing 0.5 g/100 mL sodium bisulfite (*15*), and the leaf samples were similarly extracted using 5% aqueous acetic acid (*16*). The concentrations of the individual glycoalkaloids were quantified using a high-performance liquid chromatographic method based on that of Hellenäs (*15*) and the identities of the individual glycoalkaloids were determined by liquid chromatography−atmospheric pressure chemical ionization−mass spectrometry (LC−APCI−MS) as previously reported by Griffiths et al. (*13*). Relative response factors were determined using commercially available α-solanine and α-chaconine, and the values obtained for these two compounds were also used for the quantification of α- and β-solamarine, respectively, as no commercial source of either compound was available.

Statistical Analysis. Analysis of variance, regression analysis, and the determination of correlation coefficients were carried out using Genstat for Windows, 5th edition (VSN Ltd., Oxford, UK).

RESULTS AND DISCUSSION

Tuber Glycoalkaloids. A comparison of the total glycoalkaloid content of tubers sampled immediately prior to the commencement of the light-exposure experiment with the half-tubers stored in the dark for a further 96 h (Table 2) revealed no significant differences. This would indicate that the process of halving and any associated damage of the *S. phureja* tubers did not induce any major increase in glycoalkaloid synthesis. Similar results have been reported previously for *S. tuberosum* tubers (*10*, *12*). Consequently, the increases observed in the light-exposed half-tubers must be a direct consequence of their illumination.

The levels of total glycoalkaloids in the nonilluminated *S. phureja* tubers were well below the maximum recommended value for human consumption of 20 mg per 100 g FWt (*17*). Values for two of the *S. phureja* lines (841/13 and DB 299) were slightly lower than those reported for the same two genotypes in an earlier study (*13*). Nevertheless, the relative ranking of the two genotypes was the same in both studies. This would suggest that the 50% higher values obtained in the earlier study reflected seasonal pre- and/or post-harvest environmental effects, both of which are known to modify tuber glycoalkaloid content in *S. tuberosum* (*4*, *14*).

Table 2. Effect of Light Exposure on the Total and Individual Glycoalkaloid Contents (mg/100 gFWt) of *S. Phureja* Tubers

	total[a] glycoalkaloids (mg/100 g-FWt)[b]			individual glycoalkaloids (mg/100 g-FWt)[b]				
				α-solanine		α-chaconine		α-solamarine
genotype[c]	pretreatment[d]	dark[e]	light[f]	dark	light	dark	light	light[g]
841/01	2.5	2.6	7.8	1.7	6.0	0.9	1.8	nd[h]
841/13	5.8	5.4	19.2	3.5	9.6	1.8	2.8	6.6
841/05	2.4	2.4	4.5	1.5	1.8	0.9	1.0	1.7
852/10	4.5	4.1	9.6	2.1	5.9	1.9	3.7	nd
DB 257	5.7	5.2	15.1	3.6	10.0	1.6	3.0	2.0
DB 299	3.4	3.5	13.8	2.7	4.2	0.8	1.2	8.4
DB 300	2.8	2.8	5.3	1.4	2.5	1.5	1.7	1.2
DB 323	5.7	4.8	10.0	3.7	7.5	1.0	1.5	1.0
DB 333	2.0	1.6	3.9	0.9	1.9	0.7	1.6	0.4
DB 337	3.0	3.1	5.8	2.0	3.8	1.0	1.5	0.6
DB 358	1.2	1.1	5.9	0.8	1.9	0.3	0.7	3.3
Lsd ($P < 0.05$)[i]		1.21		0.85		0.41		0.89

[a] Total = sum of all individual glycoalkaloids. [b] All values are means of single analysis from each of four replicates. [c] Abbreviated codes, see Table 1. [d] Glycoalkaloid content of tuber samples taken at commencement of light exposure experiment. [e] Glycoalkaloid content of tuber samples stored in light-proof bags under environmental conditions otherwise identical to those exposed to light. [f] Glycoalkaloid content of tuber samples exposed to light for 96 h. [g] α-solamarine was detected only in light-exposed tubers. [h] nd = not detected. [i] Least significant difference between individual means.

Light-exposure resulted in a statistically significant increase in the glycoalkaloid content of all genotypes. As previously reported (*11*) for *S. tuberosum*, the magnitude of this increase differed significantly between genotypes. The greatest increase in glycoalkaloid content was found in 841/13 which increased by almost 14 mg/100 g FWt, whereas 841/05 increased by only 2 mg/100gFWt under the same lighting conditions. Exposure to light did not result in tubers with levels above the recommended maximum concentration for human consumption. This result, however, should be interpreted with some caution as studies with *S. tuberosum* have indicated that environmental effects, in particular storage temperature, can drastically alter rates of photoinduced glycoalkaloid accumulation (*12*).

Prior to light exposure, the only detectable glycoalkaloids present in the *S. phureja* tubers were α-solanine and α-chaconine with, in all genotypes, the former predominating (Table 2). This would appear to be contrary to what is normally found in *S. tuberosum* in which the predominant glycoalkaloid in the tubers is usually α-chaconine (*9, 10*). The toxicological potency of α-chaconine has been reported as being considerably greater than that of α-solanine (*18*), possibly suggesting that at the same total glycoalkaloid concentration *S. phureja* tubers may be less toxic than those from *S. tuberosum*. Even so, synergistic effects have also been detected between both glycoalkaloids (*19*) and, consequently, without data from appropriate feeding trials, direct comparison regarding their relative toxicities cannot be made.

Light exposure increased the content of both the solanidine-based glycoalkaloids, α-solanine and α-chaconine, in all eleven *S. phureja* genotypes studied. In all cases, the greatest increase was observed in α-solanine content, which increased on average by 2.8 mg/100 g as compared with an average increase of only 0.7 mg/100 g FWt in α-chaconine content. This would appear to be consistent with results previously reported for *S. tuberosum* tubers, which also tended to synthesize relatively greater amounts of the solatriose containing the glycoalkaloid α-solanine when exposed to light (*9, 10*).

An earlier study on two *S. phureja* genotypes revealed that, in addition to the solanidine-based glycoalkaloids, light exposure also resulted in the synthesis of α-solamarine, a tomatidenol-based glycoalkaloid with a solatriose side-chain (*13*). Light exposure induced α-solamarine synthesis in nine genotypes utilized in this study, but it was not detected in quantifiable amounts in either 841/01 or 852/10 (Table 2). It is also of interest to note that quantifiable amounts of *β*-solamarine did not appear to be synthesized in response to light exposure. This glycoalkaloid contains the same aglycon as α-solamarine but instead of a solatriose carbohydrate-side-chain, is glycosylated with chacotriose. This carbohydrate group is also present in the solanidine-based glycoalkaloid, α-chaconine, which was only marginally increased in response to light exposure. However, there appeared to be no correlation between the rates of accumulation of α-solamarine and α-solanine. The identification of *S. phureja* genotypes which do not accumulate α-solamarine offers an opportunity to study both the genetics of photoinduced tomatidenol synthesis and the possibility of developing genetic markers to facilitate selection against this trait.

Leaf Glycoalkaloids. Glycoalkaloids were detected in all the leaf samples studied (Table 3). The total glycoalkaloid content was, as expected, significantly higher in the leaf samples than in the tubers. The values found ranged from 36.6 mg/100 g FWt in the leaves of genotype DB300 to over 103 mg/100 g FWt in 841/13. No statistically significant correlation was found between the amount of glycoalkaloids in the leaves with that in the tubers, either prior to or following light exposure.

An examination of the individual glycoalkaloids present in the leaves indicated that the majority of the genotypes studied contained only the tomatidenol-based glycoalkaloids, α- and *β*-solamarine (Table 3). In these genotypes, the chacotriose-containing glycoalkaloid, *β*-solamarine, was consistently the predominant glycoalkaloid. The fact that tubers from these cultivars, prior to light exposure, contained only the solanidine-based glycoalkaloids α-solanine and α-chaconine indicates that *S. phureja* tuber glycoalkaloids are synthesized in situ rather than transported from the leaves. It has previously been demonstrated using reciprocal grafts of *S. tuberosum* and *Lycopersicon esculentum* that glycoalkaloids in the former species are also produced in the

Table 3. Total and Individual Glycoalkaloid Contents (mg/100 gFWt) of *S. Phureja* Leaves and Sprouts

	leaf glycoalkaloids[a]					sprout glycoalkaloids[b]		
genotype[c]	α-solanine	α-chaconine	α-solamarine	α-solamarine	total[d]	α-solanine	α-chaconine	total[d]
841/01	31.6	56.7	nd[e]	nd	88.3	328	237	565
841/13	nd	nd	43.6	60.0	103.6	421	223	644
841/05	nd	nd	17.9	35.3	53.2	250	203	452
852/10	43.1	50.6	nd	nd	93.8	434	349	783
DB 257	nd	nd	20.2	39.1	59.3	420	206	626
DB 299	nd	nd	31.3	39.9	71.2	443	225	667
DB 300	nd	nd	12.6	24.0	36.6	328	238	565
DB 323	nd	nd	13.0	27.6	40.6	532	224	756
DB 333	3.5	6.8	9.3	21.4	41.0	205	157	362
DB 337	nd	nd	30.5	48.8	79.3	291	223	513
DB 358	nd	nd	27.0	35.4	62.4	356	184	540
Lsd ($P<0.05$)[f]	3.71	5.75	1.71	2.89	5.11	28.1	13.6	40.7

[a] Values are mean of single analysis of two replicate samples. [b] Values are mean of duplicate analysis of a single bulked sample. [c] Abbreviated codes, see Table 1. [d] Total = sum of individual glycoalkaloids. [e] nd = not detected. [f] Least significant difference between individual means.

tubers and are independent of leaf glycoalkaloid synthesis (*20*).

The leaves from two genotypes, 841/01 and 852/10, contained only the solanidine-based glycoalkaloids, α-solanine and α-chaconine, in quantifiable amounts. In both genotypes the predominant glycoalkaloid in the leaves was again the chacotriose-containing analogue, α-chaconine. It is of interest to note that the tubers from these two genotypes were also the only ones not to synthesize α-solamarine in response to light exposure. Leaf samples from one *S. phureja* genotype (DB 333) contained both the solanidine- and tomatidenol-based glycoalkaloids, and its tubers, upon exposure to light, also accumulated both types of glycoalkaloids, as did those containing only tomatidenol-based glycoalkaloids in their leaves. In a survey of a 123 commercial *S. tuberosum* cultivars, 11 were shown to accumulate solamarines when tuber slices were exposed to light during wound-healing (*21*) and, as in this study, those that accumulated solamarines also contained a high proportion of tomatidenol-based glycoalkaloids in their foliage.

Sprout Glycoalkaloids. The glycoalkaloid concentrations of the sprout samples were an order of magnitude higher than that in the leaves with the values for total glycoalkaloid content, ranging from 362 mg/100 g FWt in DB 333 to 783 mg/100 g FWt in 852/10 (Table 3). A statistically significant correlation [$R = 0.714$, $P < 0.05$] was found between tuber total glycoalkaloid content prior to light exposure and the glycoalkaloid concentration in the sprouts. As in the tubers stored in the dark, the predominant glycoalkaloid in the sprouts was α-solanine and no tomatidenol-based glycoalkaloids were detected in any of the sprout samples.

Light exposure of *S. phureja* tubers resulted in a statistically significant increase in total glycoalkaloids. In nine of the eleven genotypes studied, this increase was due to not only an increase in the solanidine-based glycoalkaloids, α-solanine and α-chaconine, but also the synthesis of the tomatidenol-based glycoalkaloid, α-solamarine, which was not detected in the tubers prior to light exposure. The identification of two genotypes that synthesized only solanidine-based glycoalkaloids will allow more detailed genetic studies to be undertaken. The glycoalkaloids present in the leaves appeared to reflect the photoinduced effects on the tubers, with those genotypes accumulating α-solamarine in their tubers also containing tomatidenol-based glycoalkaloids in their leaves.

These results may have implications for both retail outlets and for potato breeding programs. With the projected increase in the utilization of *S. phureja* germplasm in the market place, retailers will need to be made aware of the possible effects of light exposure on tuber glycoalkaloid content and, as with the more conventional tetraploid potato cultivars, should minimize, where possible, their exposure to light. Similarly, plant breeders should ensure that, when evaluating the safety to the consumer of potential commercial cultivars derived from *S. phureja*, any assessment made of the effects of light on tuber glycoalkaloid content utilizes techniques that can detect and measure both solanidine- and tomatidenol-based glycoalkaloids.

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