

Stress Metabolites of the Potato and Other Solanaceous Plants

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ABSTRACT

The effect of stress on the chemical composition of the *Solanaceae*, primarily *Solanum tuberosum* (potato), may be profound and have significant health implications. Changes in glycoalkaloids, steroids, sesquiterpenes and other lipids that result from specific and non-specific stress are discussed. The biochemistry and toxicology of these compounds are reviewed.

The terms "stress metabolite" and "phytoalexin" often have been used interchangeably, especially in discussions of disease resistance in solanaceous plants. For purposes of this review, we classify phytoalexins as a special class of stress metabolites, i.e., compounds that are not normally found in healthy tissue but accumulate in response to a disease situation and have a deleterious effect on the disease organism. Other types of stress metabolites may develop or accumulate in larger amounts than found in healthy tissue in response to nonspecific stress such as mechanical injury or environmental stress. All phytoalexins are stress metabolites but not all stress metabolites are phytoalexins. This paper reviews the chemical characterization of these compounds, their formation, their detection and what is known of their toxicity. We discuss only in passing the relationship of these compounds to disease resistance. This review covers mainly the stress metabolites of the potato (*Solanum tuberosum*), the major edible solanaceous crop on which most of the research on solanaceous stress metabolites has centered.

GLYCOALKALOIDS

Figure 1 shows the structure of α -solanine (I) and α -chaconine (II), the major glycoalkaloids of *S. tuberosum*, the species from which most cultivated potatoes in the United States and Europe are derived. The purpose of initial research on potato glycoalkaloids encompassed the development of methods to isolate, separate, identify and quantify these compounds. From the structure of α -chaconine and α -solanine, it is apparent that this class of compounds presents analytical problems in: (a) isolation due to poor solubility in most solvents and (b) detection by spectroscopy due to lack of a good chromophore. Methods described in the literature were either insensitive or nonspecific (3,9). Figure 2 summarizes the details of a titrimetric method for total

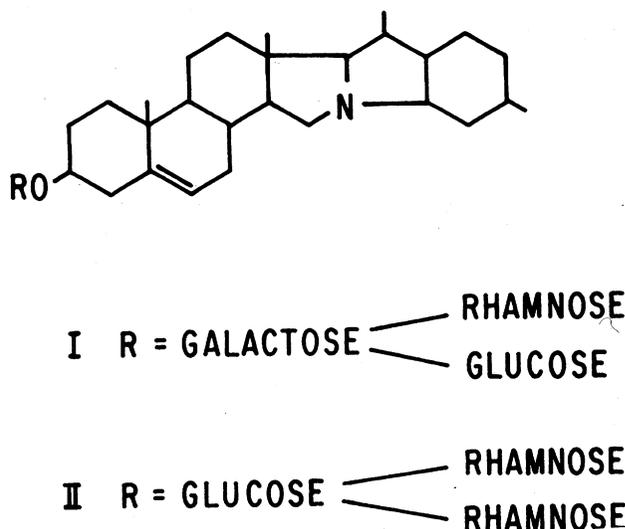


Figure 1. The major glycoalkaloids of *Solanum tuberosum*.

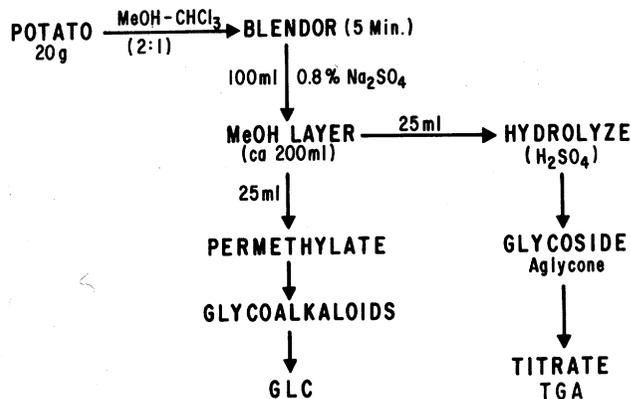


Figure 2. Quantitative and qualitative analytical procedure for potato tuber glycoalkaloids.

glycoalkaloids (TGA) (6) and a gas-liquid chromatographic (GLC) method (12) for qualitative (and relative quantitative) analysis of the individual glycoalkaloids developed in our laboratory. Figure 3 shows a GLC chromatogram of authentic glycoalkaloids. The glycoalkaloids, for qualitative and quantitative analysis, were extracted according to the procedure of Wang et al. (32). The methods we developed are specific for detection of all glycoalkaloids, whereas other methods described in the literature are either specific for a few glycoalkaloids (e.g., base insoluble or $\Delta 5$ unsaturated glycoalkaloids) or are not specific for glycoalkaloids.

We applied our procedures to studies of the glycoalkaloid composition of wild *Solanum* species and

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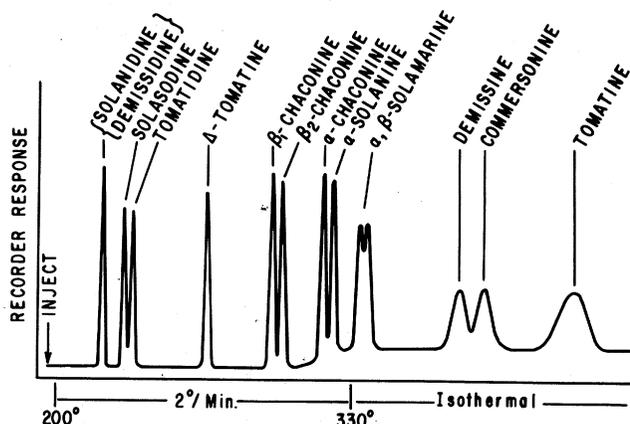


Figure 3. Gas-liquid chromatography of standard glycoalkaloids.

the effect of nonspecific stress on glycoalkaloid composition in potatoes. Our objective was to determine the inter-relationship of breeding stock and stress conditions on the control of glycoalkaloid composition and content of potatoes. The glycoalkaloid compositions of some wild *Solanum* species are summarized in Table 1. Heterogeneity was observed not only between species but also between different clones of the same species.

To dramatize the effects of mechanical stress on glycoalkaloid composition, we used potato slices as a model system. Slicing represents extreme damage that may be reflected to a lesser degree in other types of injury such as incurred in mechanical harvesting. Our investigation (7) of market potatoes revealed a number of tubers that had been cut and subsequently wound-

healed. We chose potatoes that contained only *S. tuberosum* genes and also varieties that had *Solanum demissum* in their parentage; Shih and Kuć (30) had reported the presence of solamarines in slices of cultivars derived from *S. demissum*.

In our experiments (7), facing slices were taken from the center of a potato, one slice was analyzed immediately and the other slice was analyzed after wound-healing (about 4 days at room temperature). Before being sliced, the potatoes were held under typical storage conditions (7 C and 85% relative humidity). Table 2 gives TGA levels for four commercial varieties held for extended storage periods, then sliced and analyzed immediately and after 4 days. As expected, slicing caused dramatic increases in TGA; however, the ability of slices to synthesize glycoalkaloids appears to maximize before 34 weeks of whole-tuber storage. More interestingly, storage times can significantly affect glycoalkaloid composition of damaged tubers (Table 3). After aging, Kennebec slices contained measurable quantities of α - and β -solamarine, and the level of solamarines was higher in aged slices of freshly harvested tubers than in aged slices of tubers stored for 12 or more weeks. These results indicate that damaged tubers of varieties that contain genes from other than *S. tuberosum* can have unexpected glycoalkaloid composition.

The Lenape potato, which was ready for release as a new variety about 6 years ago, rekindled interest in potato glycoalkaloids when tubers from plants grown in a greenhouse caused illness of two persons that ate them.

TABLE 1. Glycoalkaloids of selected *Solanum* species.

Species ^b	Glycoalkaloid						TGA mg/100 g FW ^e
	β -Chaconine ^c	α -Chaconine	α -Solanine	Solamarines ^a	Demissine	Tomatine	
<i>S. ajanhuiri</i>	3.5	39.0	57.3				
<i>S. curtilobum</i>		34.8	46.4	5.3	13.4		< 0.1
<i>S. stenotomum</i>	5.5	69.8	24.7				< 0.1
<i>S. juzepczukii</i>		14.0	37.8	7.7	40.4		0.7-1.3
<i>S. acaule</i> 1 ^d					95.5		1.7
2					62.1	30.9	1.4-5.0
3					88.2	11.6	1.4-5.0
4					64	34	1.4-5.0

^aCombined value for α - and β -solamarine.

^bAll species are cultivated except for *S. acaule*.

^cValues represent percent of total glycoalkaloids.

^dFour clones of species *S. acaule* were analyzed.

^eFresh weight.

TABLE 2. Total glycoalkaloid content^a of unaged and aged^b tuber slices of four varieties of stored potatoes^c.

Potato variety	Condition	Storage time of tubers before slicing					
		0 time	6 weeks	12 weeks	18 weeks	24 weeks	34 weeks
Wauseon	Unaged	3.16	5.27	4.84	3.01	3.61	5.53
Wauseon	Aged	77.88	126.43	145.85	108.24	92.45	64.38
Katahdin	Unaged	5.61	11.09	7.47	11.48	9.35	9.02
Katahdin	Aged	106.26	117.66	130.21	143.73	137.04	102.31
Houma	Unaged	3.83	6.39	4.93	3.02	3.65	7.30
Houma	Aged	58.97	51.89	34.67	84.20	95.46	61.88
Kennebec	Unaged	9.38	6.84	10.42	7.42	6.39	11.24
Kennebec	Aged	154.56	—	150.50	158.88	163.09	119.52

^aAll values expressed as mg/100 g fresh weight.

^bFour days in the dark at room temperature.

^cControlled storage, 44 F and 85% relative humidity.

Subsequently, the Lenape was found to produce higher levels of glycoalkaloids than did other commercial potato varieties, and it was withdrawn from introduction. This variety was derived from a cross between *Solanum chacoense* and *S. tuberosum*. *S. chacoense* is a heterogeneous species with respect to glycoalkaloid composition; clones have been shown to contain various combinations of α -solanine, α -chaconine, β -chaconine and leptines (28). When we undertook this study, no Lenape potatoes were available (having been withdrawn as a new variety); however, one can speculate that damaged Lenape tubers might have an interesting glycoalkaloid composition.

Although results from many laboratories, including ours, suggest that a possible health problem could result from consumption of damaged potatoes because of high and unusual glycoalkaloid composition, no systematic study has been undertaken to determine the glycoalkaloid composition of damaged market potatoes. We made a cursory study of the glycoalkaloid composition of significantly damaged tubers (8). The TGA's obtained in this experiment are given in Table 4. Higher TGA levels were found in the damaged end (A) of the tuber compared to those found in the equivalent undamaged portion (B) of the same potato; however, these differences were not large and did not appreciably affect average TGA values (C). The effects of stress on the glycoalkaloid composition of other edible *Solanaceae* such as egg plant (*Solanum melongena*) and tomato (*Lycopersicon esculentum*) have not been determined.

Levels of glycoalkaloids toxic to *Helminthosporium carbonium* were found in potato peels (1); however, Deahl et al. (5) found no correlation between levels of glycoalkaloid and late blight resistance.

The toxicity to laboratory animals of the major glycoalkaloids, α -solanine and α -chaconine, has been

measured (20,21). Although these compounds were toxic when administered intraperitoneally, they were not toxic when administered orally to mice at concentrations greater than 1 g/kg of body weight. Cardiac activity measured in a frog heart test for a number of other glycoalkaloids was similar to that of α -solanine (22). Historically, potato toxicity has been associated with glycoalkaloid concentration, although the data supporting this correlation are indirect (2). The potential for producing hazardous levels of some new glycoalkaloid does exist under the right combination of breeding and stress conditions. With the increased use of wild species in breeding programs, especially for increased pest resistance, glycoalkaloid levels and types should be carefully monitored in all parent selections to avoid years of lost research in breeding and associated financial losses.

SESQUITERPENE PHYTOALEXINS

The phytoalexins of *Solanaceae* that are produced in response to microbial infections are a class of stress metabolites that has been extensively examined in the last 10 years. About 20 phytoalexins have been identified to date. These compounds are either sesquiterpene or norsesterpene derivatives. Figure 4 shows the structures of some of the compounds that have been identified. All are potato phytoalexins except aubergene, which is a stress metabolite of *S. melongena*, and capsidiol, which is a stress metabolite of *Nicotiana* and *Capsicum bructesceus* (goat pepper). All these compounds can be shown to arise from cyclization of farnesyl pyrophosphate to yield the proper intermediate. A likely intermediate leading to most of these structures would be the eudesmane skeleton (Fig. 5) proposed by Stoessl and Ward (31). Sato et al. (27), however, recently demonstrated that the spiro compound oxylubimin (Fig. 4) is

Table 3. Percentages of the major glycoalkaloids in unaged vs. aged tuber slices from potatoes stored at 44 F.

Storage (weeks)	Wauseon				Houma			
	Unaged		Aged ^a		Unaged		Aged ^a	
	α -chac ^b %	α -sol ^c %	α -chac ^b %	α -sol ^c %	α -chac ^b %	α -sol ^c %	α -chac ^b %	α -sol ^c %
0	74.6	25.4	49.6	50.4	69.0	31.0	50.0	50.0
6	68.7	31.3	44.4	55.6	67.2	32.8	48.3	51.7
12	66.2	33.8	40.6	59.4	68.1	31.9	43.2	56.8
18	86.0	14.0	44.8	55.2	74.5	25.5	46.1	53.9
24	80.1	19.9	44.0	56.0	71.8	28.2	42.5	57.5
34	73.3	26.7	43.4	56.6	70.1	29.3	40.1	59.9

Storage	Katahdin				Kennebec					
	Unaged		Aged ^a		Unaged		Aged ^a			
	-chac ^b	α -sol ^c	α -chac ^b	α -sol ^c	α -chac ^b	α -sol ^c	α -chac ^b	α -sol ^c	β -sola ^d	α -sola ^d
0	64.1	35.9	42.7	57.3	58.9	41.1	24.9	37.1	11.5	26.5
6	58.4	41.6	37.2	62.8	54.9	45.1	26.8	33.3	12.4	27.5
12	60.8	39.6	38.5	61.5	52.3	47.7	24.3	43.4	8.3	24.0
18	65.2	34.8	35.3	64.7	59.8	40.2	28.2	44.6	6.8	20.5
24	67.0	33.0	36.5	63.5	63.9	36.1	26.6	54.0	4.6	14.8
34	65.0	35.0	38.0	62.0	57.7	42.3	23.8	56.0	5.6	14.6

^aFour days in dark room at ambient temperature.

^b α -Chaconine.

^c α -Solanine.

^dSolamarines (found only in aged Kennebec slices).

the precursor of rishitin. Shih et al. (29) suggested that the formation of sesquiterpenes may result at the expense of steroid synthesis. Although the importance of these compounds in disease resistance is still not clear, they do result from what is termed the hypersensitive or incompatible host-parasite interaction. They can be formed also in nonhypersensitive interactions (such as *Erwinia caratovora* var. *atroseptica* vs. *S. tuberosum* (17,18)) in which the typical indicators of hypersensitivity, necrotic lesions, are not observed. Nonspecific inducers of these compounds such as NaF (19) have been reported.

A number of other unidentified stress metabolites arise from fungus- or fungal extract-inoculated potato slices, but these are found in much smaller quantities than the compounds shown in Fig. 4.

The anti-fungal (10) and anti-bacterial activities (16) of rishitin and other potato phytoalexins have been investigated. Although they are fungistatic, these metabolites when sprayed on leaves did not reduce the incidence of late blight, whereas capsidiol sprayed on tomato leaves significantly controlled *P. infestans* development (33).

Stress metabolites were implicated as teratogens when Renwick (25), a well-known British epidemiologist,

proposed a correlation between blighted potato consumption by mothers and the birth defects spina bifida and anencephaly in their offspring. Although some initial experimental evidence (23) supported this hypothesis, more extensive experiments including feeding studies with potato tubers high in the phytoalexins rishitin and phytuberin did not confirm the original conclusion (24). Keeler et al. (13) indicated that potato sprouts may contain materials teratogenic to the golden hamster. The toxicity of the potato phytoalexins has not been investigated comprehensively; however, solavetivone (katahdinone) has been tested in a chick embryo bioassay and found to be nontoxic (4). We intend to determine the toxicity of many of these compounds, if they can be isolated in sufficient amounts for meaningful evaluation.

NONSPECIFIC STRESS COMPOUNDS

While the phytoalexins are generally formed by a specific stress (i.e., fungal infection), nonspecific stress, as already mentioned, also can produce these compounds. Nonspecific stress is responsible for many more chemical alterations in the *Solanaceae* besides changes in glycoalkaloid levels or formation of phytoalexins. Many of these changes, including stimulated phenolic synthesis

TABLE 4. Glycoalkaloid analysis of bruised commercial potatoes.

Cultivar	Sample ^a	Fresh wt (g)	Dry powder (g)	Solids (%)	mg TGA/100 g fresh wt
Katahdin	1-A	112.3	23.8	21	16.5
	1-B	147.7	29.5	19	6.3
	1-C	92.3	18.0	19	13.4
	2-A	65.5	13.6	20	14.5
	2-B	53.8	18.7	34	9.2
	2-C	94.0	11.7	12	8.4
	3-A	97.4	20.2	20	19.5
	3-B	129.8	25.0	19	15.0
	3-C	110.0	22.0	20	11.2
	4-A	61.1	12.4	20	19.3
	4-B	101.0	18.2	18	10.2
	4-C	110.0	20.2	18	10.0
	Russet Burbank	5-A	113.0	28.0	24
5-B		111.0	24.7	22	1.5
5-C		110.0	22.0	20	3.1
6-A		47.0	13.5	28	7.2
6-B		57.0	13.6	23	1.5
6-C		59.0	15.0	25	6.1
7-A		198.5	49.0	24	7.6
7-B		119.6	23.2	19	2.5
7-C		88.1	20.0	22	3.3
8-A		45.2	9.2	20	5.5
8-B		80.0	16.6	20	1.8
8-C		40.0	7.4	18	5.3
Red Pontiac		9-A	114.6	21.5	18
	9-B	123.6	21.5	17	2.3
	9-C	73.4	13.0	17	4.9
	10-A	122.0	21.0	17	6.9
	10-B	95.5	18.0	18	1.8
	10-C	87.5	14.0	16	2.1
	11-A	162.0	35.5	21	7.5
	11-B	133.0	26.0	19	4.6
	11-C	73.0	14.0	19	12.1
	12-A	79.5	14.0	17	6.07
	12-B	73.0	14.0	19	2.58
	12-C	51.0	10.0	19	6.26

^aA = damaged end; B = center section; C = undamaged end.

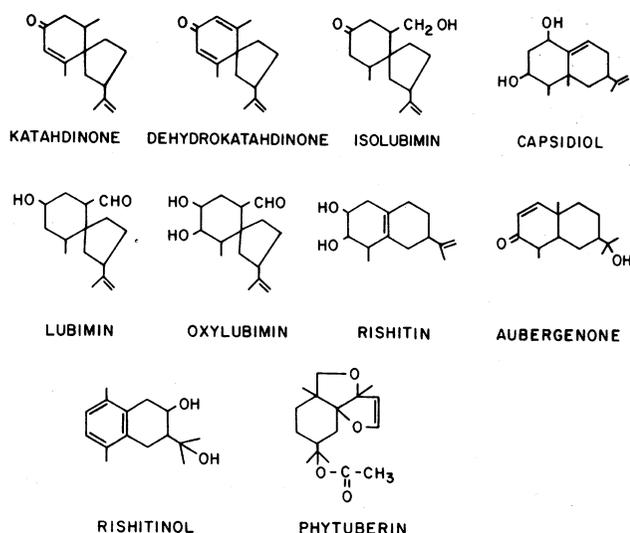


Figure 4. *Sesquiterpene phytoalexins.*

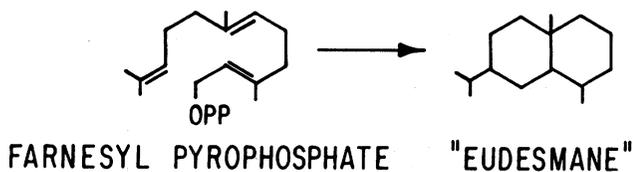


Figure 5. *Biosynthetic pathway for phytoalexins.*

(such as chlorogenic acid and scopoletin) and suberization, have been defined. Such chemical alterations have been observed because of the ease of detection of these compounds. The extent of damage to fruits and vegetables due to mechanical harvesting and handling necessitates a more comprehensive examination of the chemical composition of these commodities. Toward this end, we analyzed the tuber slice system for compositional changes other than those previously observed. Initially, we examined that fraction of tuber tissue that contains the plant sterols. Hartmann and Benveniste (11) reported the rapid increase of sterols in aged potato slices. This also was observed in our study; however, a much more dramatic chemical distinction was noted when extracts from incubated potato slices were compared with fresh potato extracts. The C-28 alcohol, octacosanol, which could not be found in the fresh extract, was isolated in relatively large amounts from the incubated slices (Table 5). The rate at which octacosanol is formed is shown in Fig. 6. A lesser amount of n-hexacosanol also was isolated, but no other fatty alcohols (C₁₆-C₃₀) could be detected in either fresh or aged slices (15). Suberin, which is rapidly formed during wound healing, contains esters of fatty alcohols in its structure (14). However, only traces of octacosanol were found after deesterification of suberin. Octacosanol may have a physiological function similar to that reported for triacontanol in alfalfa (26). Preliminary results in our laboratory indicate that this compound also may affect host-parasite interactions.

Stress may alter chemical composition via catabolic processes, for example, by stimulating hydrolase activity. In our investigation of the *E. caratovora* var. *atroseptica*-*S. tuberosum* interaction, appreciable amounts of

TABLE 5. *Sterol^a content of fresh and aged potato slices.*

Sterol	μg / g f.w. ^b	
	Fresh	4 days aged ^c
Cholesterol	0.1	0.42
n-octacosanol	< 0.1	3.94
Stigmasterol	0.38	1.50
β-sitosterol	0.56	1.60

^aMajor sterols.

^bFresh weight.

^cIn dark.

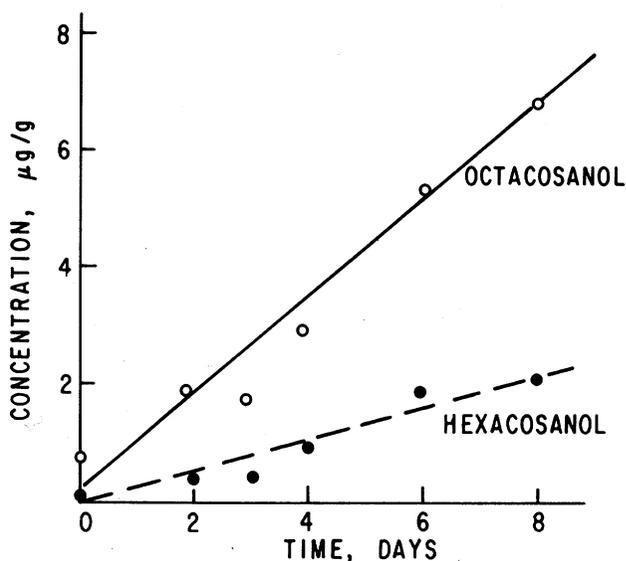


Figure 6. *Production of octa- and hexacosanol in potato slices.*

solanidine, the aglycone of solanine and chaconine, were recovered (34). Solanidine is not found in unstressed tuber tissue. The hydrolase activity apparently resides in the tuber, since microwaved slices (that contain solanine and chaconine) do not yield solanidine when treated with this species. Other hydrolytic products of glycoalkaloids also have been identified in nonspecifically disrupted tissue (29).

In this review we attempted to show the complexity of chemical changes that occur when plant tissue is stressed. Although abundant information on the chemical composition of healthy plant tissue is available, we know much less about the composition of this tissue at the time of consumption, when many chemical alterations may have occurred due to stress. These chemical alterations may have significant human health implications and therefore warrant further investigation.

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