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Glycoalkaloid change during the domestication of the potato, *Solanum* Section *Petota*

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Summary

The hypothesis that selection for reduced toxicity occurred as part of the domestication of the potato was investigated by analyses of the total glycoalkaloid (TGA) content of 30 accessions of 8 species of reputed wild progenitors of *Solanum tuberosum* and *S. stenotomum* and 12 accessions of 5 species of edible wild potatoes. Although mean TGA content of tubers of likely ancestoral species varied from 24–96 mg/100g, the most likely progenitor (*S. sparsipilum*) had the highest glycoalkaloid content (range 40–164; mean 96 mg/100 g). Three of the five wild species known to have been eaten historically had potentially toxic TGA content. Mexican *S. cardiophyllum* and *S. ehrenbergii,* however, contained almost no glycoalkaloids. The individual glycoalkaloids are reported for each of the accessions studied. The results indicate that the above hypothesis can be accepted.

Introduction

Potentially toxic glycoalkaloids likely precluded other than the casual exploitation of the tubers of most wild species of potatoes by humans. Total glycoalkaloid content in potatoes is highly heritable (Sanford & Sinden, 1972) and an apparent aspect of the domestication of members of *Solanum* Series *Tuberosum* in the Central Andes was the selection by humans for genotypes with reduced levels of glycoalkaloids. This assumption, which underlines our previous investigations in this area, has not been adequately tested. Indeed, to the contrary, the exploitation of tubers of wild *S. cardiophyllum* Lindl. in Mexico today without any form of processing or resulting toxicity suggests that species of *Solanum* with low content of glycoalkaloids existed before domestication and could have been the progenitors of cultivated potatoes.

The suppression of plant protective mechanisms such as thorns, spines and chemical defenses is a general phenomenon during domestication (Hawkes, 1983). In this paper we test the hypothesis that progenitors of *S. stenotomum* Juz. et Buk., *S. tuberosum* L. and other potato cultigens were sufficiently high in glycoalkaloids to necessitate a process of chemical selection. Firstly, we look at the glycoalkaloid content of wild tuber-bearing species of *Solanum* that have been consumed historically. Secondly, we test the hypothesis directly by examining the glycoalkaloids of species of *Solanum* that are possible progenitors of cultivated potatoes.

Elevation of glycoalkaloid content can be a problem when wild species are used in potato breeding programs. Assessment of glycoalkaloid levels is important for determining the suitability of particular wild species for such programs (Gregory et al., 1981).

Edible wild species of potatoes

Although over 150 species of *Solanum* Section *Petota* are known from North and South America (Hawkes, 1978) there are historical records of only a few of these being consumed on a regular basis. Previous studies of glycoalkaloid content in tubers of wild potatoes report values ranging from 20–126 mg/100 g fresh weight (Johns and Osman, 1986; Osman et al., 1978), with values typically about 50 mg/100 g.

Solanum maglia

Solanum maglia Schlechtd. is reported to have been a food of the Araucanian Indians of Central Chile although this has not been authenticated with proper botanical identifications. While Laufer (1938) called *S. maglia* the chief article of food of the Araucanians, the source he cites (Latcham, 1904) spoke only of the wild potato with its Araucanian name, *poñi*. The most detailed studies of the food plants of these people fail to mention wild potatoes at all (Alvarez, 1963; Cooper, 1946) or give them a minor place in the Araucanian diet (Hilger, 1957). In the modern era, at least, most of the potatoes eaten by the Araucanians are cultivated *S. tuberosum*.

Ugent et al. (1987) reported fragments of potato tubers from the archaeological site, Monte Verde, occupied about 13,000 years ago. Based on starch grain analyses they identified these as *S. maglia* and argued that they formed part of the diet of the Late Pleistocene inhabitants of this site.

Descriptions of *S. maglia* differ as to the bitterness of the tubers. Correll (1962) confirmed the assessment of De Candolle (1886) in describing the tubers of this species as mostly bitter, while Ugent et al. (1987) attest that none of them are bitter.

Ugent et al. (1987) revive arguments that Chile is a place of origin of *S. tuberosum* (subsp. *tuberosum*), the potato of global commerce, with *S. maglia* as a possible progenitor. Diploid and triploid forms of *S. maglia* are known from the wild. The theoretical original form of *S. tuberosum* would be a tetraploid derived through a spontaneous doubling of the chromosomes of diploid *S. maglia*. This scenario has been discounted by others (Hawkes, 1978).

Solanum jamesii and *S. fendleri*

Solanum jamesii Torr. and *S. fendleri* Gray are part of the traditional diet of the Hopi (Whiting, 1939), Navajo (Bailey, 1940), Zuni (Cushing, 1920), Tarahumara (Bye, 1976; Pennington, 1963) and other indigenous peoples in the American Southwest and northern Mexico. In Arizona and New Mexico these plants were protected and often encouraged as weeds in maize fields. They were usually harvested during periods of seasonal scarcity (Palmer, 1871; White, 1945).

Historical reports indicate that these tubers are bitter and their consumption can result in severe gastrointestinal disturbances and vomiting (Johns, 1986). To combat the toxic effects of these potatoes native peoples usually consumed them with edible clays. Geophagy appears to be an effective means to adsorb glycoalkaloids in these potatoes (Johns, 1986).

The Tarahumara of Chihuahua State, Mexico, cultivate a wild potato (*rerówi*) which Bye (1976) identified as *S. fendleri*. Pennington (1963) suggests that this species is 'on the verge of domestication'. It is regarded as having a good taste, suggesting perhaps that some selection has already taken place for clones with low glycoalkaloids.

Solanum cardiophyllum

Solanum cardiophyllum and *S. ehrenbergii* (Bitt.) Rydb. (*S. cardiophyllum* subsp. *ehrenbergii* Bitt.) have been extensively consumed in Mexico since ancient times. They occur as weeds in maize fields in the Central Mexican states of San Luis Potosi, Aguascalientes and Zacatecas, are harvested when the fields are plowed, and are sold in markets of that region. Local sources, including an old text published in San Luis Potosi (without a date) by P.O. Cabera, suggest that in the sixteenth century these tubers, called *cimatli* in the Nahuatl language, were an important food source for the Chichimeca and Aztec peoples of the region. The Tepehuán Indians of Chihuahua States gather tubers of *S. cardiophyllum* from the wild and eat them after boiling (Pennington, 1969). These species are invariably described as non-bitter and edible (Correll, 1962) and in Central Mexico are highly apreciated.

It is thus an enigma why Mexican Indians who domesticated many species including maize, beans, tomatoes and squashes did not domesticate *cimatli.* Toxic or unpalatable constituents appear not to be the reason. Experimental attempts to cultivate *S. cardiophyllum* failed because of attacks by *Alternaria tenuis* and *Phytophthora infestans* (Galindo A., 1982); apparently because of this susceptibility to pathogens humans have had to continue to gather these tubers from wild scattered populations.

Glycoalkaloids in Cultivated Potatoes

Eight taxa of cultivated potatoes are consumed in South America and feral varieties of *S. tuberosum* are gathered occasionally in both Mexico and South America. With the exception of two hybrid species, cultivated potatoes usually have total glycoalkaloid (TGA) content less than 15 mg/100 g, although levels may increase during storage or under extreme weather conditions (Sinden et al., 1984). In contrast with other cultigens, *S.* X *juzepczukii* Buk. and *S.* X *curtilobum* Juz. et Buk. are bitter and potentially toxic. As a result they are usually consumed after detoxification processing (Johns & Kubo, 1988) or with edible clay (Johns, 1986). Total glycoalkaloid content of these tubers varies between 12 and 64 mg/100 g (Johns, 1990; Osman et al., 1978).

Glycoalkaloids at these levels do not pose a complete barrier to direct human consumption. Immediately postharvest, the Aymara eat tubers of the bitter cultigen, *S.* X *juzepczukii*, without processing (simply boiled) (Johns & Keen, 1985) or as *lojoto* or *chuño fresco* (Mamani, 1981). To prepare *lojoto* frozen tubers are thawed and squeezed before boiling. Elimination of the juice may significantly reduce the alkaloid content of these bitter potatoes.

Among diploid cultigens the highly variable *Solanum stenotomum* is considered ancestral. The most likely progenitors of *S. stenotomum* include *S. canasense* Rydb. (including *S. soukupii* Hawkes), *S. leptophyes* Bitt., *S. multiinterruptum* Bitt., *S. sparsipilum* (Bitt.) Juz. & Buk. (Ugent, 1970). All of these species are placed in Series *Tuberosum* (Hawkes, 1978). Other members of this series that may have been contributed genes to the early cultigens include *S. brevicaule* Bitt., *S. bukasovii* Juz., *S. multidissectum* Hawkes, *S. spegazzinii* Bitt., and *S. vidaurrei* Cárd.; none of these species have been studied for tuber glycoalkaloids. Ugent (1970) suggests that *S. raphanifolium* and *S. megistacrolobum* may have contributed to the gene pool of cultivated potatoes. We have examined the glycoalkaloids of these and other members of Series *Megistacrolobum* previously (Johns & Osman, 1986).

Cribb & Hawkes (1986) argue that *S. tuberosum* subsp. *andigena* (Juz. et Buk.) Hawkes, the reputed ancestoral potato tetrapoid, arose through a process of allopolyploidy involving *S.stenotomum* and *S. sparsipilum.* Progeny produced in hybridization experiments supported this hypothesis.

S. X *ajanhuiri* Juz. et Buk. is a cultigen derived from hybridization between *S. stenotomum* and wild *S. megistacrolobum* Bitt. Comparison of glycoalkaloid content of clones of this species and its wild and cultivated relatives (Johns & Osman, 1986) with biosystematic data from this group (Johns et al., 1987) supports the argument that selection for glycoalkaloids has taken place in the evolution of *S.* X *ajanhuiri*. Based on this result we hypothesize that at the onset of the domestication of potatoes selection for decrease in glycoalkaloid content would have been an important step.

Materials and methods

Twelve wild species of *Solanum* were analyzed for TGA and for the identity of individual glycoalkaloids. All analyses for TGA were carried out on tubers. Material designated by PI accession numbers was obtained from the Potato Introduction

Station, Sturgeon Bay, Wisconsin. Material was freeze-dried and stored at − 20° C. The single sample of *S. maglia* (PI 208563) was from a diploid accession that was experimentally doubled to the tetraploid level (R. Hanneman, unpublished results).

Field collection of tubers of *S. cardiophyllum* were made in Mexico and preserved in 95% methanol.

Included in the study was fresh tuber material of a wild potato collected at Nutria on the Zuni Reservation, New Mexico, in July, 1984, by Richard I. Ford.

Qualitative identification of glycoalkaloids only was carried out on leaves of one accession of *S. leptophyes* (PI 320341) grown at the Matthaei Botanical Gardens, University of Michigan, from seeds obtained from the Potato Introduction Station.

The extraction and analysis procedures for the indentification of ammonia precipitable glycoalkaloids by thin-layer and gas chromatography and the determination of TGA content by titration were as described in Johns and Osman (1986).

Results and discussion

Glycoalkaloid characteristics of the edible North American species of potato are contained in Table 1. Results of the analyses of South American species of *Solanum* Section *Petota* are in Table 2.

Glycoalkaloids in potatoes are generally regarded as toxic in levels above 20 mg/100 g TGA (Gregory, 1984; Jadhav et al., 1981). This value is somewhat arbitrary in that quantity and frequency of consumption as well as patterns of nutrition and exposure to other environmental factors will determine the toxicity to a particular consumer. Nonetheless, in situations where potatoes are a staple food, levels much above 20 mg/100 g would undoubtedly impose a constraint on the routine con-

Table 1. Glycoalkaloids of Species of Wild Potatoes Consumed Historically in North America

Species and Accession	Collection location	TGA mg/100 g	Aglycones as % of total				Glycoalkaloids
			1	2	3	4	
S. cardiophyllum							
PI 186548	Zac-MEX	2					
sc1	MEX	2					
sc2	MEX	1					
sc3	MEX						dem*
sc12	MEX	2					
S. ehrenbergii							
PI 275216	Quer-MEX						dem*
PI 347759	Pueb-MEX	6					dem*
S. fendleri							
PI 255531	Mich-MEX	64	100	0	0	0	α-sol, α-chac
PI 255543	Sin-MEX	69	100	0	0	0	α-sol, α-chac
S. jamesii							
PI 275263	USA	128	0	0	0	100	tom
.....	Zuni	115	0	0	0	100	–

* Best guess based on TLC data only.

Country Codes: MEX, Mexico; USA, United States of America. State Codes: Mich, Michoacan; Pueb, Puebla; Quer, Queretaro; Sin, Sinaloa; Zac, Zacatecas.

Aglycones: 1 = solanidine; 2 = demissidine; 3 = tomatidenol; 4 = tomatidine.

Glycoalkaloids: chac = chaconine; dem = demissine; sol = solanine; tom = tomatine.

Table 2. Glycoalkaloids of possible progenitors of *Solanum stenotomum* and *S. tuberosum*

Species and Accession	Collection location	TGA mg/100 g	Aglycones as % of total				Glycoalkaloids
			1	2	3	4	
S. brevicaule							
PI 498110	Coch-BOL	44	100	0	0	0	α-sol. α-chac
PI 498111	Coch-BOL	23	100	0	0	0	α-sol, α-chac
S. bukasovii							
PI 473492	Huan-PER	9	100	0	0	0	α-sol, α-chac
PI 473493	Huan-PER	28	100	0	0	0	α-sol, α-chac
PI 473494	PER	29	100	0	0	0	α-sol, α-chac
PI 498219	Jun-PER	25	100	0	0	0	α-sol, α-chac
PI 498220	Jun-PER	29	100	0	0	0	α-sol, α-chac
S. canasense							
PI 310940	Cuz-PER	62	92	8	0	0	dehy, dem
PI 310941	Cuz-PER	47	93	7	0	0	dehy, dem
PI 442696	Puno-PER	78	100	0	0	0	α-sol, α-chac
PI 473355	Aya-PER	43	100	0	0	0	α-sol, α-chac
S. leptophyes							
PI 320341	BOL						
(foliar glycoalkaloids)							α-sol, α-chac
PI 473445	Cuz-PER	42	94	6	0	0	dehy, dem
S. maglia							
PI 208563	ARG	56	100	0	0	0	α-sol, α-chac
(tetraploid)							
S. multiinterruptum							
PI 275272	PER	42	0	0	0	100	tom, dem?
PI 498265	Anc-PER	68	100	0	0	0	α-sol, α-chac
PI 498266	Anc-PER	50	100	0	0	0	α-sol, α-chac
S. raphanifolium							
*PI 310951	Cuz-PER	37	100	0	0	0	α-sol, α-chac
*PI 310999	PER	28	100	0	0	0	α-sol, α-chac
PI 458383	Cuz-PER	30	100	0	0	0	α-sol, α-chac
PI 458406	Cuz-PER	70	100	0	0	0	α-sol, α-chac
PI 458407	Cuz-PER	60	100	0	0	0	α-sol, α-chac
S. sparsipilum							
PI 498131	Coch-BOL	127	100	0	0	0	α-sol, α-chac
PI 498132	Coch-BOL	40	100	0	0	0	α-sol, α-chac
PI 498134	Coch-BOL	92	100	0	0	0	α-sol, α-chac
PI 498282	Lpz-BOL	62	100	0	0	0	α-sol, α-chac
PI 498283	BOL	92	100	0	0	0	α-sol, α-chac
PI 498305	Cuz-PER	164	100	0	0	0	α-sol, α-chac

* from Johns and Osman, 1986.

Country Codes: ARG, Argentina; BOL, Bolivia; PER, Peru. Department Codes: Anc, Ancash; Aya, Ayacucho; Coch, Cochabamba; Cuz, Cuzco; Huan, Huancavelica; Jun, Junin; Lpz, La Paz; Puno, Puno.

Aglycones: 1 = solanidine; 2 = demissidine; 3 = tomatidenol; 4 = tomatidine.

Glycoalkaloids: chac = chaconine; dehy = dehydrocommersonine; dem = demissine; sol = solanine; tom = tomatine.

sumption of these tubers. Levels above approximately 20 mg/100 g become unpalatable (Johns & Keen, 1986; Sinden et al., 1984) to humans.

Using these criteria most of the wild tubers of potato examined in this study are potentially toxic and unpalatable. The North American species, *S. jamesii* and *S. fendleri*, with TGA content from 64–128 mg/100 g are, as human behavior suggests, inedible without some method of detoxification.

Although there is no historical evidence that wild potatoes except *S. maglia* were consumed in the South America for other than emergency food, the availability of techniques to detoxify cultivated potatoes high in glycoalkaloids does not rule out that wild species even with high glycoalkaloid were consumed in quantity prior to the domestication of this species. Certainly, if humans did select for reduction in glycoalkaloid content during domestication, some degree of technology would have been necessary to allow humans to interact with toxic potatoes in the first place. Alternatively, the progenitor of cultivated potatoes could have been species or populations that are naturally low in glycoalkaloids.

If the tubers of the clone of *S. maglia* analysed in this study with 56 mg/100 g TGA are representative, glycoalkaloids would be a constraint to human use of this species. No mention of processing or of geophagy is made in the reports on the use of this species by the Araucanians. Tubers with glycoalkaloid content in this range may have been exploited on a casual basis, particularly if they were peeled. Because glycoalkaloids are concentrated in the outer layers of a potato, peeling may remove 30% or more of the total amount present in a tuber (Woolfe, 1987).

If the potato was domesticated from one or more species with low levels of glycoalkaloids, selection for glycoalkaloid content in tubers that were only marginally edible would become unnecessary as an explanation of the domestication of the potato. The low levels of glycoalkaloids in Mexican *S. cardiophyllum* and *S. ehrenbergii* is consistent with the suggestion that nontoxic edible potatoes exist in the wild. Consistent with our expectations all accessions of *S. cardiophyllum* and *S. ehrenbergii* examined in this study, including both field collected material and that grown at the Potato Introduction Station, were nontoxic. In fact most of the tubers we examined had levels < 4 mg/100 g TGA. While individual accessions of a particular species have been reported with such low glycoalkaloid levels (Johns & Osman, 1986) we know of no other species with such consistently low TGA content.

The presence of α-solanine and α-chaconine as the major glycoalkaloids of accessions of wild species of *S.* Series *tuberosum* from the Central Andes was consistent with the occurrence of these compounds in *S. stenotomum* and *S. tuberosum.* A few individual accessions varied from this pattern, although all except PI 275272 (*S. multiinterruptum*) contained the solanidine aglycone typical of this series. *S. raphanifolium* is unique among members of series *Megistacrolobum* in containing these same compounds, suggesting introgression of genes from Series *Tuberosum* into this species via the cultivated gene pool (Johns & Osman, 1986). None of these accessions had total glycoalkaloid content as low as the Mexican species described above. One species, *S. bukasovii,* with 9–29 mg/100 g TGA(mean = 24 mg/100 g TGA) was consistently close to the levels found in many clones of *S. stenotomum.* Exploitation and domestication of this species would require little or no selection for glycoalkaloid content.

Accessions studied of the most likely progenitors of *S. stenotomum (S. canasense, S. leptophyes, S. multiinterruptum,* and *S. sparsipilum*) ranged in TGA level from 40–164 mg/100 g with a mean value of 68 mg/100 g. Domestication from any of these species required some reduction in TGA.

The scenario for the domestication of *S. tuberosum* involving hybridization of *S. stenotomum* and *S. sparsipilium* followed by a doubling of the ploidy level is complicated by the high TGA of *S. sparsipilum* (40–164 mg/100 g; mean = 96 mg/100 g). If this species was involved in the origin of *S. tuberosum,* selection for reduced levels of glycoalkaloids among the hybrid progeny of *S. stenotomum* and *S. sparsipilum* has likely taken place.

The nature of wild species of potato in the Central Andes may have changed during domestication as germplasm of the cultigens introgressed into them or as they hybridized among themselves in an anthropogenic environment (Ugent, 1970). The glycoalkaloid content of wild species through this process would be expected to stay the same or be reduced. While it may not be realistic to pinpoint a true ancestor of the potato, the consistently high TGA content of Andean potatoes indicates that selection for these compounds has taken place between the wild and the cultivated.

Reduction of TGA during the domestication processs need not necessarily be direct; selection for increased tuber size could reduce the concentration of TGA relative to increase in water and carbohydrate. Either selection for size or for reduced toxicity could have been primary, although co-selection for both characteristics is a reasonable explanation for these crucial domestication events.

The best evidence for chemical selection in the domestication of the potato can come from situations where the phylogeny of a taxon is supported independently. Biosystematic data in conjunction with TGA data involving *Solanum* × *ajanhuiri* and *S. tuberosum* offer strong support for the hypothesis that detoxification was an important aspect of the evolution of the potato crop.

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