GENETIC AND ENVIRONMENTAL CONTROL OF POTATO GLYCOALKALOIDS

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Abstract

Genetic and environmental factors that can cause potato tubers and processed products to have excessive glycoalkaloid levels (> 20 mg/100 g fresh wt) are reviewed and discussed. Measures that breeders, growers, processors, and distributors might take to maintain glycoalkaloid levels at their present low levels are suggested.

Resumen

Se revisan y se discuten los factores genéticos y ambientales que pueden producir niveles excesivos de glicoalcaloides (> 20 mg/100 g de peso fresco) en los tubérculos de papa y los productos procesados. Se sugieren medidas que puedan tomar los fitomejoradores, agricultores, técnicos en procesamiento y distribuidores para mantener bajos los niveles de glicoalcaloides.

Introduction

Potato tubers normally contain 1 to 15 mg/100 g fresh wt of the glycoalkaloids solanine and chaconine. At these low levels solanine and chaconine do not affect culinary quality, nor do these low levels present any health hazard to the consumer. However, glycoalkaloid levels in potatoes subjected to certain environmental stresses can rise from the normal 1-15 mg level to 20 mg or higher (3, 4, 51, 65, 67). And some experimental cultivars, because of their unusual genetic backgrounds, regularly synthesize contents in excess of 20 mg/100 g (43, 46, 51, 68).

It is important that glycoalkaloids be maintained at their present low levels in new commercial cultivars brought to the consumer and in tubers and potato products of present commercial cultivars for the following reasons: 1. Glycoalkaloid levels above 20 mg/100 g have a noticeable, adverse effect on flavor (4, 26, 41, 53). 2. Glycoalkaloids have no known positive role in human nutrition; the known and suggested effects of even small quantities of these natural toxicants are all negative (20, 69). 3. Illnesses and even a few deaths have been attributed to the consumption of potatoes with glycoalkaloid contents in excess of 28 mg/100 g (4, 19, 27, 29, 63).

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4. There are reports that some types of glycoalkaloids, including solanine, may have teratogenic activity in certain animals (5, 23, 24, 32). Even though there may be no sound scientific basis for the allegations that glycoalkaloids can be harmful, an increase in levels, or introduction of new forms of these natural toxicants into future varieties, could generate adverse publicity for the potato.

It should not be difficult to maintain levels below 20 mg/100 g, the upper limit for complete safety suggested by Bomer and Mattis (4) in 1924 and generally accepted as a safe upper limit throughout the world. Ross et al. (41) consider 6-7 mg/100 g to be the maximum acceptable content because of the effects of glycoalkaloids on flavor. And Wilson (63) suggested 20-25 mg/100 g as the safe upper limit on the basis of his review of the literature and the illnesses he investigated that were caused by eating potatoes with a content of 40 mg/100 g. Certainly, for flavor considerations alone, it would appear desirable to market potatoes and potato products with less than 20 mg/100 g of glycoalkaloids.

Tuber contents in commercial potatoes rarely exceed 20 mg/100 g. In the few instances where excessive contents in a particular crop have been discovered and the causes investigated, unusual environmental stresses and/or an unusual ancestry of the cultivar have been suspected of causing the high contents. Most of the known causes of excessive glycoalkaloid levels are factors that can easily be controlled by the breeder, the grower, or those involved in processing and marketing.

Environmental Control

It appears that almost any stress that affects growth and development of the crop can also have some effect on the glycoalkaloid content. Climate, altitude, soil type, soil moisture, fertilization (see 19, 27, 52 for reviews), air pollution (56), time of harvest, vine-killing (9), pesticides (64), and sunlight exposure (4, 18, 31) of tubers are all reported to affect total glycoalkaloid (TGA) levels of tubers at harvest. Exposure of harvested tubers to light (4, 7, 16, 17, 19, 38, 41, 67), mechanical damage (1, 10, 28, 65), and time and temperature of storage (4, 9, 66) are among the several factors and treatments reported to affect post-harvest TGA levels (19, 27, 52). Most of these stresses and treatments do not cause whole-tuber TGA contents to increase to levels above 20 mg/100 g. As there seems to be no reason for concern with TGA levels that fall within the 1-15 mg range, and thus no reason to attempt to control levels in this range, only those stresses and genetic factors which may be capable of inducing contents to rise above 20 mg/100 g in marketed tubers or potato products will be given major consideration in this review. Comprehensive reviews of the many factors in the growing environment and the numerous post-harvest treatments affecting TGA levels in potatoes have previously been published (19, 27, 52).

Tuber glycoalkaloid contents vary widely among crops of a single cultivar produced under various growing environments (4, 26, 41, 52), and even among the tubers from a single plant (66). The smaller tubers in a hill generally have higher contents because of the way glycoalkaloids are distributed within a tuber (66). The outer layers of the tuber, particularly the epidermis and cortex, have much higher contents than the pith tissue (3, 16, 25, 65). Since smaller tubers have a higher ratio of skin and cortex tissue to pith tissue, smaller tubers will tend to have higher contents simply because of the unequal distribution of glycoalkaloid concentrations within the tuber. For instance, contents in tubers of 'White Rural' ranged from 7.3 in 270 g tubers to 18 mg/100 g in 31 g tubers from the same plot (65). The contents of small (< 40 g) immature tubers from 8 French cultivars ranged from 10 to 45 mg/100 g, and most of the samples of these small tubers had contents greater than 20 mg/100 g (61).

Peels generally have contents in excess of 20 mg/100 g (3, 6, 16, 17), and peels usually contain more than half of all the glycoalkaloid content in the tuber even though the peel comprises less than 20% of the total tuber wt (3, 4, 6, 67). Therefore, peeling will usually reduce the contents of small, high-glycoalkaloid tubers to levels considered perfectly safe (4). Very small potatoes with their skins intact are sometimes preferred for certain specialty dishes home-gardeners prepare. Only small quantities of these tiny tubers are included in the specialty dishes, so glycoalkaloid content is not a health consideration. For economic reasons, commercial growers usually allow tubers to fully size and reach maturity before harvest.

Immature tubers, irrespective of their size, apparently tend to have higher glycoalkaloid contents than fully mature tubers (4, 9, 31, 51, 52, 61, 66). Bomer and Mattis (4) found contents of 26 to 58 mg/100 g in 80 to 100 g tubers of six separate samples of the 1922 German potato crop that caused many illnesses. Tubers of comparable size from the 1923 crop had contents below 10 mg/100 g. After investigating the possible effects that greening, fertilization, size, and maturity might have on contents, these researchers concluded that the higher than normal levels in the 1922 crop were caused by a general immaturity of this crop. Cool weather, a large number of overcast days, and heavy rainfall in 1922 apparently inhibited the normal bulking and maturation process, and caused much of the crop to be quite immature when it was harvested.

Immaturity, caused by extended day-lengths coupled with cool temperatures and a short growing season, may also have been responsible for the excessive TGA levels in some Alaskan potatoes (52). 'Kennebec', 'Russet Burbank', and 'Katahdin' from Palmer, Alaska had TGA contents of 29-36 mg/100 g in 1971, and 13-22 mg/100 g in 1970. Wolf and Duggar (66) noted a general decline in the glycoalkaloid contents of tubers of 3 varieties as they matured over a 52 day period. However, it was not clear from their results

how much of this decline was due to increases in tuber size with advancing maturity, and how much was due to changes in rates of synthesis and/or degradation of glycoalkaloids. Cronk et al. (9) reported small decreases in two varieties and a small increase with maturity in a third variety they harvested at 118 vs 146 days after planting. However, 118 days of culture would usually be sufficient for most varieties to reach full maturity, so the increase and the decreases between 118 and 146 days may have been caused by factors other than maturity differences in this study.

Light induces glycoalkaloid synthesis in tubers and prolonged exposure of tubers to sunlight is a well-known cause of excessive TGA levels. Even relatively short exposures of harvested tubers to intense sunlight can cause large increases in TGA levels. Baerug (3) reported that TGA content increased from 5 to 20 mg/100 g after only 6 hrs of exposure of harvested tubers to direct sunlight with a Norwegian variety used to study the relationship between flavor, TGA contents, and light exposure. Zitnak (67) found levels as high as 45 mg/100 g in 'Netted Gem' tubers exposed for only 72 hrs to intense sunlight under near freezing temperature conditions following harvest. The TGA contents of tubers left on top of the soil for 3 months after harvest were compared with those of tubers stored in the dark after harvest (41). Tubers exposed to sunlight developed contents 1.7 to 5.2 fold higher than those stored in the dark; the magnitude of the increase depended on the variety. Major varietal differences in glycoalkaloid synthesis in response to light exposure were also noted in a study of greening and glycoalkaloid synthesis in New Zealand potato varieties (38).

Immature tubers are more likely to develop excessive TGA levels upon exposure to sunlight than mature tubers (4, 38). Immature tubers of 7 varieties generally developed excessive TGA levels after 18 days' exposure to indirect sunlight, with a range of contents from 6.6 to 48 mg/100 g, depending on the variety. In contrast, none of the 7 varieties had levels above 20 mg/100 g when mature tubers were exposed to the same light conditions for an even longer period, 22 days (38).

Glycoalkaloids apparently do not diffuse from the green, light exposed, high TGA portion of a tuber to the unexposed portions. Bomer and Mattis (4) removed the soil cover from the upper half of attached tubers, allowing sunlight exposure of the upper halves for one month during the growing season. The green, sunburned halves had a content of 19 mg/100 g, whereas, the unexposed portions of the same tubers had a content of 3.8 mg/100 g.

Artificial light such as tubers might be exposed to during storage or marketing can also induce glycoalkaloid synthesis (3, 4, 16, 17, 19, 66). However, either because the artificial light is not as intense as sunlight, or, because the artificial light sources do not emit ultraviolet radiation to any great extent, there are few reports of whole-tuber TGA levels in excess of 20 mg/100 g arising from exposure to artificial light sources (17). The ultraviolet portion

of the light spectrum may be more effective than the higher wavelengths in inducing glycoalkaloid synthesis, according to Connor (7). Therefore, greening which can be induced by low levels of artificial light (3, 7, 19), is not necessarily an indication that the tubers have excessive TGA contents, particularly if the greening is superficial. And, removal of the green portion of tubers that become sunburned in the field will usually lower the TGA content of the remaining portion to an acceptable level.

Diffuse sunlight can filter through an inadequate layer of soil and induce some greening and glycoalkaloid synthesis even if tubers are covered with soil. Potatoes planted with only minimal soil cover and not hilled up during the growing season tend to form higher glycoalkaloid levels than those planted deeply and kept well covered (18). Because of grading standards for green tubers and the possible high glycoalkaloid levels that could result from inadequate soil cover, growers should always protect tubers from sunlight exposure by providing sufficient soil cover to prevent greening and sunburning. U.S. potato grading standards state that if more than 5% of the weight must be removed to eliminate the greened tissue, the tubers are damaged; if the removal exceeds 10% of the weight, the product is seriously damaged (19). These grading standards were developed, in part, to protect consumers from excessive glycoalkaloid consumption, and are rigorously enforced in some localities.

Genetic Control

Glycoalkaloid content varies widely among commercial cultivars and the average content a cultivar synthesizes is probably controlled by genes inherited from the cultivar's ancestors (26, 41, 42, 51, 68). Although significant interactions between variety and environment have been demonstrated (51), a cultivar that synthesizes relatively high levels under one set of environmental conditions will tend to have high levels wherever it is grown (26, 51, 52). And cultivars with high average contents are more likely to synthesize levels in excess of the 20 mg/100 g limit when subjected to stresses or improper handling. For instance, 'Kennebec', with an average content of 9.7 mg/100 g over 39 locations in the U.S. in 1970, synthesized contents greater than 20 mg/100 g at 3 of the 39 locations. In contrast, 'Red Pontiac', with an average content of 4.3 mg/100 g, synthesized contents no greater than 9 mg/100 g at any of the 39 locations (52).

In surveys of commercial cultivars grown around the world (3, 4, 17, 26, 31, 38, 41, 50, 57, 60, 66), contents are reported to range from a low of 1.1 (41) to 35 mg/100 g (3). TGA contents of 32 American varieties surveyed in 1946 ranged from 2 to 13 mg/100 g (66). In a survey of 58 German varieties grown at 6 locations in 1948, contents ranged from 2 to 22 mg/100 g (26). Various methods of analysis were used in the surveys, and in some of the surveys the reported contents were determined by sampling tubers from only one growing environment. Nevertheless, from all the available reports on

TGA contents of commercial cultivars from around the world, and taking into account the possible sampling and analytical errors, it is clear that most commercial cultivars usually have TGA contents of less than 20 mg/100 g.

It was discovered in 1970 that a new American cultivar, 'Lenape', had an average TGA content of 27 mg/100 g over 10 locations in Canada (68) and a similarly high average content of 29 mg/100 g over 39 locations in the U.S. (51). Under stress conditions such as those that occurred at one location in the U.S., the TGA content of 'Lenape' rose to 65 mg/100 g, a potentially hazardous level (52). The content of 'Kennebec', a variety that normally synthesizes relatively high levels of glycoalkaloids, was elevated from its national average of 9.7 mg/100 g to only 16 mg/100 g by these same stress conditions (52). 'Lenape' was removed from commerce in 1970 because of its tendency to regularly synthesize glycoalkaloid contents in excess of the accepted 20 mg/100 g limit.

'Lenape' has an unusual ancestry for a commercial cultivar in that *Solanum chacoense,* a high glycoalkaloid wild species, was used as a source for improved yield, solids, and chipping quality in the breeding of this cultivar (2). The glycoalkaloid level in the *S. chacoense* clone that appears in the pedigree of 'Lenape' is not known and cannot be determined because this particular clone is no longer available. Nor is the hybrid grandparent (Menominee × *S. chacoense*) or the male parent (hybrid × 'Cherokee') of 'Lenape' still available. But there is considerable indirect evidence that this *S. chacoense* ancestor was the source of the abnormal TGA content found in 'Lenape', as hypothesized by Zitnak (68).

Glycoalkaloid analyses of foliage and tubers of various collections of *S. chacoense* show that levels in this wild species are generally 5 to 100 times higher than those found in *S. tuberosum* (14, 30, 44, 54). *S. chacoense* is rarely used in potato breeding. However, when this species was used as a source of resistance to the Colorado potato beetle in a breeding program in Germany in the 1950's, tubers from resulting hybrids and F_2 populations were generally high in TGA contents and many of the clones had TGA contents in excess of 20 mg/100 g (46, 47). When 'Lenape' was crossed with 'Houma' and a sample of 20 offspring analyzed for tuber TGA, the offspring had an average TGA content of 19.4 mg/100 g with a range of 3-37 mg/100 g among the 20 offspring. 'Houma' tubers had a TGA content of 10.3 mg/100 g while 'Lenape' tubers had a TGA content of 37 mg/100 g in this study of the inheritance of TGA contents (42). Thus, it appears that 'Lenape' inherited genes for synthesis of higher than normal TGA levels from its *S. chacoense* ancestor and that 'Lenape' can transmit genes for excessive levels of glycoalkaloid synthesis to a portion of its offspring.

Heritability estimates of tuber glycoalkaloid content from a two-year study of 10 cultivar crosses in a varietal breeding program show that glycoalkaloid levels are highly heritable in tetraploid *S. tuberosum* (42).

Estimates ranged from 86-89% in a broad sense, and from 64-84% in the narrow sense. Offspring variations within families were generally continuous, indicating polygenic inheritance of TGA levels. Ross et al. (41) estimated heritability of TGA in the broad sense at 25-26% from the tuber contents they measured in a 4-year, variety-location study. Thus it appears that once very high TGA levels are introduced from wild species gene sources into parental lines in a breeding program, higher than normal levels will persist among some of the offspring. Therefore, wild species with very high glycoalkaloid levels should be used with caution in breeding. And when high levels are introduced through hybridization, glycoalkaloid analyses of selected offspring may be necessary in order to maintain normal levels of TGA among potential varieties in the breeding program.

Many wild, tuber-bearing *Solanum* species and most cultivated South American species used in potato breeding as sources of desirable genes for frost resistance, pest resistance, or improved yield and quality have relatively low TGA levels (36, 44, 45). Among these low TGA species are *S. phureja, S. tuberosum* (ssp. *andigena*), *S. stoloniferum, S. veruccosum,* and *S. stenotomum*. Tubers of *Solanum* species are frequently smaller than those of *tuberosum* cultivars. As Wolf and Duggar (66) point out, glycoalkaloid contents of tubers are of little value for comparative purposes unless tuber size is taken into account. Thus, the reported TGA contents of species tubers may sometimes be higher than those for commercial cultivars. However, when the small size of the tubers is taken into account, the TGA levels in most *Solanum* species are about the same as, or lower, than those of commercial cultivars. And, commercial cultivars with species ancestors do not generally have a higher or lower TGA content when compared with those of pure *tuberosum* descent (11, 41).

Wild species such as *S. chacoense,* with 5-10 times the TGA levels in their tubers and foliage compared to *tuberosum* cultivars, could, however, present problems for breeders attempting to maintain low TGA levels in their breeding stocks and varietal releases. Tubers of *S. commersonii* were found by Wolf and Duggar (66) to have a content of over 500 mg/100 g, and they cautioned breeders to "look with suspicion at this species as a source of improved quality or resistance." Among other wild species in which at least one accession of the species has foliar glycoalkaloid levels more than 5 times higher than the levels in *tuberosum* cultivars are: *S. brachycarpum, S. hjertingii, S. hougasii, S. kurtzianum, S. medians, S. pinnatisectum* and *S. polyadenium* (14).

At least one accession of most wild species available to the breeder has been analyzed for glycoalkaloid level and composition in one of several surveys (14, 15, 36, 43, 44, 45, 58, 59). These surveys can be helpful in determining whether or not a wild species being considered for use in a breeding program is especially high in TGA. Certain wild species are apparently quite

polymorphic for both TGA levels and the types of glycoalkaloids present among individual accessions of the species (14, 30, 35, 43, 59). For instance, tubers from a natural hybrid between *S. berthaultii* and *S. tarijense* had contents ranging from 6-432 mg/100 g, among 6 accessions surveyed (59). Therefore, the reported TGA levels in a species may not be consistent with the actual TGA level of a particular accession of the species. And it may be necessary to analyze a range of accessions or the particular accession considered for hybridization in a breeding program to avoid later problems with elevated TGA levels in hybrid and backcross generations.

Ross (40) considered the high TGA levels found in some wild species to be of no consequence to breeders because he felt that suppression of glycoalkaloid synthesis is a dominant trait and that most cultivars have two or more dominant alleles for low TGA synthesis. No experimental data to support this contention were presented, however, and the limited quantitative data that are now available do not seem to suggest dominance of low TGA levels (12, 13, 30, 39, 42, 43). In reviewing the literature available to 1978 on inheritance of glycoalkaloids in hybrid crosses, McCollum and Sinden (30) concluded that there was evidence for both dominance and non-dominance of genes for high levels from wild species, but no evidence for complete dominance of low levels. Quantitative data obtained in glycoalkaloid inheritance studies involving crosses between wild species and *tuberosum* cultivars can be difficult to interpret, especially when tuber levels are reported, because of the diversity of tuber sizes from species, hybrids, and cultivars. The analytical method can be important because some wild species contain other types of glycoalkaloids that are not quantitatively detected with the commonly-used methods of analysis (8, 14, 15). And, the potential for aneuploidy in offspring of hybrids between species differing in chromosome number can affect the genetic interpretation.

In the most comprehensive study to date of the inheritance of glycoalkaloid levels in a hybrid between a high glycoalkaloid wild species, *S. caldasii,* and a *tuberosum* cultivar, Georgieva and Ronkov (12) found that hybrid tubers had an average TGA level ca 10 fold higher than the *tuberosum* parent. The average content of hybrid tubers was reduced considerably, to only ca 5 fold higher than that of 'Deodara', the *tuberosum* parent, by one backcross. One of the 7 backcross progeny had a TGA content as low as that of 'Deodara', indicating that it should be possible to obtain low TGA cultivars from high TGA hybrids without extensive backcrossing.

All that would be necessary, apparently, to release a variety with normal TGA content from a hybrid breeding program such as that studied by Georgieva and Ronkov would be a limited number of glycoalkaloid analyses, coupled with selection of clones with normal TGA. In that regard, the variety 'Seminole' with normal TGA content is a sib of 'Lenape'. In repeated analyses of 'Seminole' tubers over 3 years, TGA contents never exceeded 12 mg/

100 g. Also, the new variety 'Atlantic' (62) has 'Lenape' as its male parent, and 'Atlantic' has not produced TGA contents in excess of 18 mg/100 g in samples taken from 2 locations over 2 years. However, because of its 'Lenape' parentage, 'Atlantic' was not released to growers until repeated analyses showed that it synthesized normal TGA levels (unpublished results). TGA analyses of cultivars derived from high-TGA wild species that are being considered for release to growers would appear to be advisable until more is known about the transmission of TGA levels in hybrid crossing programs. Simple and reliable methods for rapid TGA determination are now available (8).

A high TGA *Solanum* species cultivated in some localities in the Andes is a putative natural hybrid between a high-TGA, tetraploid, wild species, *S. acaule,* and a low-TGA, cultivated, diploid species, *S. stenotomum.* The hybrid, *S. juzepczukii,* had tuber TGA contents ranging from 18 to 49 mg/100 g, in analyses of 15 accessions. *S. acaule* had contents ranging from 53-123 (5 accessions), whereas, the putative low-TGA parent had 3-5 mg/100 g (2 accessions). These results (43) likewise seem to suggest that high TGA levels can be transmitted from high-TGA wild species to hybrids. Interestingly, while *S. juzepczukii* is extensively cultivated in several localities in the Andes because of its frost resistance, the tubers are too bitter to eat. The glycoalkaloids are removed by a leaching process in the production of chuno for consumption (43).

Many of the species used in potato breeding synthesize only solanine and chaconine, e.g., *S. phureja, S. tuberosum* (spp. *andigena*), *S. vernei* and *S. stoloniferum* (44, 45). However, some wild sepecies synthesize other types of glycoalkaloids in addition to, or in place of, the usual solanine and chaconine. For instance, while many accessions of *S. chacoense* synthesize only solanine and chaconine (30, 44), certain other accessions synthesize leptines and leptinidines in addition to solanine and chaconine (14, 45, 54). Other accessions of *S. chacoense* synthesize only commersonine, or a mixture of commersonine and demissine, instead of solanine and chaconine (30, 35). Two species that have been used as sources of disease and frost resistance, *S. demissum* and *S. acaule,* respectively, synthesize demissine and tomatine instead of solanine and chaconine (36, 43, 45). Solamargine and solasonine (14, 59), and α-solamarine and β-solamarine (14, 36, 43, 59) are among other forms of glycoalkaloids reported to be present in major amounts in one or more of the tuber-bearing Solanum species. The nomenclature and biochemistry of the potato glycoalkaloids is somewhat complex. Excellent reviews of the glycoalkaloids in tuber-bearing Solanum species include those by Osman (37) and Schreiber (45).

Other types of glycoalkaloids have not been found in more than trace quantities in healthy tubers of commercial cultivars. And, while other glycoalkaloids may be no more hazardous or bitter than solanine and chaconine,

discovery of their presence in tubers of future commercial cultivars could possibly result in questions being raised about the safety and palatability of such potatoes. The various types of glycoalkaloids found in potato species are known to differ in their physiological and toxicological effects on experimental animals (5, 20, 33, 34). Rather than attempt to prove that other types of glycoalkaloids that might be introduced from wild species into commercial cultivars through breeding are as safe as solanine and chaconine, it might be more prudent, and easier, to exclude other glycoalkaloids from new, species-derived varieties.

Foreign glycoalkaloids can be transmitted from wild species to hybrids (13, 39, 43). In the case of demissine in hybrids between *S. demissum* and *S. tuberosum,* the demissine was eliminated after only two backcrosses to *tuberosum* (13). The presence of tomatine from the *S. demissum* parent in the hybrids was not reported. However, the methods these researchers used to determine presence and quantities of demissine would not have differentiated tomatine from demissine, if tomatine were present.

There is circumstantial evidence that the foreign solamarines found in leaves of 'Kennebec' by Shih and Kuc (49) were transmitted to this commercial cultivar from its *S. demissum* ancestor. Solamarines are also found in wound-healed tissues of 'Kennebec' tubers, but not in healthy tubers. The solamarine glycoalkaloids have the same sugar moieties as solanine and chaconine, but the sugars are linked to a foreign aglycone, tomatidenol, instead of to the solanidine aglycone of solanine and chaconine. Shih and Kuc postulated that 'Kennebec' inherited the ability to synthesize this foreign aglycone from its *S. demissum* ancestor. If the gene(s) for tomatidenol synthesis in 'Kennebec' were indeed inherited from the *S. demissum* ancestor of Kennebec, then the gene(s) persisted through at least 5 backcrosses to recurrent *tuberosum* (55). Thus, it may not always be possible to prevent the introduction of foreign glycoalkaloids from wild species into new commercial cultivars without selecting against foreign glycoalkaloids.

Results from an inheritance study of solamarines in *tuberosum* cultivars suggest that tomatidenol synthesis in 'Kennebec' and some other solamarine synthesizing cultivars is controlled by a single major gene, possibly inherited from *S. demissum* (55). Four other commercial cultivars with the same *S. demissum*-derived parent as 'Kennebec' also synthesize solamarines. And, this *S. demissum*-derived parent of 'Kennebec,' X-96-56, which is the source of the R_1 gene for late blight resistance, and appears in the pedigrees of at least 36 other American varieties, also synthesizes solamarines. A commercial cultivar with only putative *tuberosum* ancestors was found among the 9 commercial cultivars identified as solamarine synthesizers in a survey of 123 commercial cultivars. Thus, the origin of the gene(s) for solamarine synthesis in commercial cultivars is not certain.

Schmiediche et al. (43), found high levels of the solamarines in the hybrid *S. juzepczukii.* Neither of the progenitor species of *S. juzepczukii* synthesized even trace amounts of these unusual glycoalkaloids. They therefore concluded that, as in the case of the solamarines in 'Kennebec,' the solamarines in the hybrid were synthesized by the recombination of sugars and aglycones from the progenitors. However, in contrast to the missing demissine and tomatine parental glycoalkaloids in 'Kennebec' and X96-56, all the accessions of *S. juzepczukii* they surveyed synthesized all four parental glycoalkaloids, in addition to the non-parental solamarines. The glycoalkaloid composition of *S. juzepczukii* illustrates the complexity of the glycoalkaloid situation that could occur with certain hybrid breeding programs. Each of the progenitors of this natural hybrid synthesizes only two glycoalkaloids. At least 6 different glycoalkaloids are present in the hybrid (43).

Single genes appear to control the synthesis of the various types of sugar moieties found among the potato glycoalkaloids, at least in diploid *S. chacoense.* McCollum and Sinden (30) found simple segregation ratios of 3:1 in an F_2 and 1:1 in backcross generations for presence: absence of solanine, chaconine, and commersonine in a study of the inheritance of glycoalkaloid types in *S. chacoense.* In offspring of crosses between species that differ in the types of glycoalkaloids synthesized, genes controlling the type of sugar moiety can apparently recombine with genes controlling the type of aglycone synthesized. This recombination of genes in F_1, F_2, and backcross generations can result in synthesis of new types of glycoalkaloids, types not synthesized by either of the parents in the cross (30).

The synthesis of solamarines by X96-56 and 'Kennebec' may serve as an example of recombination of separate genes for aglycones and sugars in hybrid offspring with the resultant synthesis of new, non-parental types of glycoalkaloids. *S. demissum* does not synthesize solatriose or chacotriose, the sugar moieties of α- and β-solamarine, respectively. Nor does *S. demissum* synthesize tomatidenol, the aglycone of the solamarines. Rather, *S. demissum* synthesizes tomatidine, which differs from tomatidenol by being saturated at the Δ^5 bond of the steroid molecule, and demissidine, the saturated form of solanidine (37, 45). *S. demissum* also synthesizes lycotetraose, the sugar moiety of both demissine and tomatine. All *S. tuberosum* cultivars synthesize solatriose, chacotriose, and solanidine, but most do not synthesize major amounts of tomatidenol, such as the amounts found in X96-56 and 'Kennebec' (55).

α-Solamarine is formed from the glycosidic linking of tomatidenol and solatriose, whereas β-solamarine is tomatidenol linked to chacotriose (37, 45). If Shih and Kuc (49) are correct in their hypothesis that 'Kennebec' inherited the ability to synthesize solamarines from *S. demissum,* then *S. demissum* must have provided the gene(s) for synthesis of the tomatidine steroid aglycone. But, tomatidenol is synthesized in 'Kennebec', not

tomatidine. Therefore, a gene(s) from Kennebec's *tuberosum* ancestors for dehydration of the Δ^5 bond in the aglycone moiety must be present and expressed in 'Kennebec,' as well as genes for solatriose and chacotriose. Apparently the gene(s) from *S. demissum* for saturation of the Δ^5 bond of the aglycone, as in demissidine and tomatidine, and the gene(s) for lycotetraose synthesis are recessive in 'Kennebec' or have been lost in backcrossing, as 'Kennebec' does not synthesize saturated aglycones or the tometetraose sugar moiety. Thus, solamarines in commercial cultivars could have arisen from the recombination of a gene(s) for tomatidine from *S. demissum* with a gene(s) for dehydration of the Δ^5 bond from *tuberosum,* and genes for synthesis of solatriose and chacotriose from *tuberosum.*

The non-parental glycoalkaloids dehydrocommersonine, dihydrosolanine, dihydrochaconine, and saturated and unsaturated forms of the leptines are probably the result of the new gene combinations in an F_2 population of *S. chacoense* derived from two parents that differed in the types of glycoalkaloids they synthesized (54). It was not clear, though, whether the separate genes for sugar and aglycone type are entirely independent (30).

The available evidence therefore suggests that foreign glycoalkaloids from wild species, or at least the sugar or aglycone moieties of these foreign glycoalkaloids, could appear in new varieties derived from species with unusual types of glycoalkaloids. The recent bridging of natural crossing barriers by geneticists (21) and cell biologists (48) could create combinations of aglycones and sugars not now present in any *Solanum* species. The mere presence of solanine and chaconine in potatoes has for many years been a matter of concern because of the known toxicological properties of steroidal glycosides as a class of compounds. Certain types found in *Veratrum* species are especially potent and should never be introduced into any food, e.g., jervine and cyclopamine (22).

Additional glycoalkaloid inheritance studies with wild species and their *tuberosum* hybrids appear to be necessary to learn more about the potential, or lack of potential, for introducing new types of glycoalkaloids into the food chain. Until such time as it is definitely established that new types will not appear in commercial cultivars derived from wild species with unusual forms of glycoalkaloids, qualitative analyses of selected hybrids, backcross clones, and potential releases would appear desirable. Methods for such analyses are available (8, 14, 15), but additional research is needed to develop methods more applicable to the large numbers of samples from a breeding program.

Conclusions

Glycoalkaloid levels in tubers of commercial crops rarely exceed the suggested limit for complete safety, 20 mg/100 g fresh wt. The environmental stresses that can cause levels to rise above 20 mg/100 g are for the most part known and easily controlled by the grower or those involved in processing

and marketing potatoes. Varieties differ widely in the average contents they synthesize. Contents are highly heritable, and the breeder can control the levels in new varieties by the appropriate selection of wild species and parental cultivars. Analyses of selected hybrids and potential varietal releases may be necessary to maintain normal glycoalkaloid levels when certain wild species are used in breeding. New types of glycoalkaloids with known toxicological properties could occur in future varieties derived from wild species with unusual forms of glycoalkaloids unless qualitative analyses of glycoalkaloid composition of hybrids and potential varieties are conducted. While glycoalkaloid levels and types in present commercial varieties offer little cause for concern, additional research, and some caution in breeding with wild species, will help to ensure the safety of future varieties.

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