Glycoalkaloid Content in *Solanum* Species and Hybrids from a Breeding Program for Resistance to Late Blight (*Phytophthora infestans*)

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ABSTRACT

As part of an effort to study the relationship between the "glycoalkaloid trait" and genetic resistance to late blight (*Phytophthora infestans*), glycoalkaloid content in tuber and foliar tissues from a wide genetic background within *Solanum*, including *S. demissum*, *S. iopetalum* and 15 hybrids selected from a backcrossing breeding scheme was determined. Analysis of variance indicated significant genotypic effect on total glycoalkaloid, solanidine, α-solanine, and α-chaconine content in both tubers and leaves. Tubers from wild potato species commonly contain glycoalkaloids in concentrations that exceed international health regulations for human consumption (20 mg/100 g fresh weight). In this study, *S. demissum* and *S. iopetalum* were highest in total tuber glycoalkaloids among all materials tested, with 70.4 and 76.2 mg/100 g fresh weight, respectively. In contrast, both commercial cultivars had the lowest concentration, both below the safety limit. Solanine was more abundant than chaconine in all but one genotype. All hybrids were intermediate to low in total glycoalkaloids. Except for the two wild species, glycoalkaloid concentration in leaves of all genotypes studied was at least twice that in tubers, with glycosylated forms accounting for more than 80% total glycoalkaloid content. Correlation between tuber and foliage alkaloids was poor. In view of the observed field resistance to late blight, it was concluded that tuber glycoalkaloid content may not be responsible for such resistance.

INTRODUCTION

Wild potato (*Solanum*) species are commonly used in breeding programs searching for resistance to pathogens, insects, and other forms of environmental stress. Use of these species, however, can be potentially hazardous to human health since, together with the desired resistance, other related traits such as a high glycoalkaloid content can be transferred during the breeding process (van Gelder and Scheffer 1991; Friedman and McDonald 1997). Glycoalkaloids are naturally ocurring toxins of steroid nature known to cause poisoning and even death in humans (Morris and Lee 1984). Damage at the cellular level involves membrane stability properties as a primary target (Coria *et al.* 1998). Many of the *Solanum* species that are of interest to breeders may contain levels of total glycoalkaloids in excess of 20 mg/100 g fresh weight, the standard maximum level allowed by international health regulation (Gregory 1984). Among solanaceous glycoalkaloids, α-chaconine and α-solanine are the most abundant (95%) in the potato plant, in which all tissues have been reported to produce them from mevalonate via cholesterol; the steroidal core, solanidine, is glycosylated by solatriose or chacotriose to yield solanine or chaconine, respectively (Stapleton *et al.* 1991). Some other alkaloids can occur in wild potato species, which can be transmitted to hybrids; in the case of demissine in hybrids between *S. demissum* and *S. tuberosum*, demissine was effectively eliminated after only two backcrosses to *tuberosum*, and the presence of tomatine from the *S. demissum* parent in the hybrid–if at all present–was not distinguished from that of demissine (Sinden *et al.* 1984). Thus, by and large, both qualitatively and quantitatively, the importance of solanine and

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TGA, total glycoalkaloids; TLC, thin layer chromatography; RC, backcrossing cycles.

chaconine overrides that of any other alkaloid in the potato plant.

The content of different glycoalkaloids in the potato plant varies both qualitatively and quantitatively according to genetic and environmental influences, including exposure to light (Deahl *et al.* 1991; Dale *et al.* 1993), mechanical damage, and extreme storage temperature (Maga 1980; Woolfe 1987). These observations have led to the belief that glycoalkaloids may be resistance-related factors developed by the plant to cope with damage caused by pathogens and insects (Gregory 1984). In vitro tests have shown that glycoalkaloids inhibit mycellium growth and production of spores in several fungi (Allen and Kuc 1968; Moore and Orcutt 1982), as well as larval development and leaf and tuber consumption by adult insects (Fewell and Roddick 1993). However, a recent review by Friedman and McDonald (1997) has concluded that the exact role of glycoalkaloids in the resistance of potato to attack from pathogens of various kinds is still undefined.

In addition to their higher glycoalkaloid content, the wild and primitive potato genetic resources contain different forms of these toxins, which make the outcome of hybrid combinations unpredictable, particularly due to poorly understood synergistic effects among the variants. Therefore, care must be taken in the development of new varieties of potato that glycoalkaloid content does not rise to unsafe levels, or that new more toxic glycoalkaloids are not introduced into commercial germplasm. The present study was conducted to determine glycoalkaloid content in foliage and tuber tissue from the parental wild and commercial clones and 15 hybrids from three cycles of backcrossing from a breeding scheme aimed at obtaining a new variety with resistance to late blight (*Phytophthora infestans*).

MATERIALS AND METHODS

Plant Material

Genetic material used in these studies included the following: two wild potato species, *S. demissum and S. iopetalum*, both used as donors of resistance to late blight; two commercial clones of *S. tuberosum*, Alpha and Lopez, both of which are highly susceptible to late blight; one advanced clone with a high degree of resistance to the disease, 78-199-33; one resistant variety named IRERI; and 15 different hybrids from the second, third, and fourth cycles of backcross. All genetic material was kindly donated by the National Potato Program of the Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP) in México. Table 1 presents the genetic background of the 15

TABLE 1.—*Genealogy of* Solanum tuberosum *x* Solanum *hybrids used to determine glycoalkaloid content.*

BC2 group	L = López susceptible cv.
1	E-91-64-1 iop = (BC1-177 x 77-69-43) = (321 x L—pez)-3 x L—pez)-1 x 77-69-43
2	E-91-80-6 dms = (BC1-87 x Granola) = (246 xL—pez)-6 x L—pez)-1 x Granola
3	E-91-20-6 dms = (BC1-65 x 77-1A-11) = (258 x L—pez)-7 x L—pez)-1 x 77-1A-11
4	E-91-32-5 dms = (BC1-17 x 77-1A-11) = (209 x L—pez)-5 x L—pez)-1 x 77-1A-11
5	E-91-78-1 iop = (BC1-224 x Granola) = (266 X L—pez)-3 x L—pez)-3 x Granola
BC3 group	
6	E-92-17-50 dms = (E-91-30-6 x L—pez) = (BC1-66 x 77-1A-11) x L—pez) = (258 x L)-7 x L)-1) x 77-1A-11) x L—pez.
7	E-92-17-28 dms = (E-91-30-6 x L—pez) = (BC1-66 x 77-1A-11) x L—pez) = (258 x L)-7 x L)-1) x 77-1A-11) x L—pez.
8	E-92-10-10 dms = (E-91-71-5 x L—pez) = (BC1-15 x 77-1A-11) x L—pez) = (209 x L)-5 x L)-1) x 77-1A-11) x L—pez.
9	E-92-18-5 iop. = (E-91-5-5 x L—pez) = (BRA-745 x 77-69-43) x L—pez) = BC1.
10	E-92-7-14 iop. = (E-91-37-5 x L—pez) = (BC1-184 x L—pez) x L—pez) = (322 x L)-1 x L)-1) x L—pez) x L—pez.
BC4 group	
11	E-94-8-10 iop = (E-92-14-5 x ASN-69-1) = (E-91-36-5 x L) x ASN) = (BC1-224 X L) x L) x ASN) = ((266 x L)-3 x L)-3 x L) x ASN-69-1.
12	E-94-10-34 iop = (Michoac‡n x E-92-14-49) = Mich x (E-91-36-5 x L) = Mich x (BC1-224 x L) x L = Mich x (266 x L)-3 x L)x L) x L.
13	E-94-16-41 iop = (Cruza 114 x E-92-16-20) = C-114 x (E-91-35-1 x L) = C-114 x (BC1-175 x 720055) x L = C-114 x (321 x L)-3 x L) x 720055) x L.
14	E-94-26-16 dms = (E-92-13-5 x 77-18-335) = E-91-15-5 x L) x 77-18-335) = (BC1-122 x 212-91) x L) x 77-18-335 = (73 x L)-4 x L) x 212-91) x 77-18-335).
15	E-94-31-26 dms = (E-92-10-9 x 77-18-335) = (E-91-71-5 x L) x 77-18-335) = BC1-111 x Granola) x L) x 77-18-335 = (299 x L)-2 x L) x Granola) x L) x 77-18-335.

hybrids from various backcrosses and Figure 1 summarizes schematically the original cross between donors and recipient of late blight resistance and the backcrossing cycles (BC groups).

Crop Planting and Culture

Sprouted tubers from each material were planted in a field in the Toluca Valley experimental station of INIFAP (19° 30' NL, 2,840 masl) on June 2, 1997, under rainfed conditions. The site is characterized by endemic high innoculum pressure from *P. infestans* every year; for this reason it is regarded as the site of choice to test for resistance to late blight. Standard culture practices within the station were followed to prepare the land and plant the crop. Fertilizer and fungicides were applied according to standard station management to the advanced and commercial clones, but not to the wild parents nor to the backcrosses. The experimental area was divided into 10 sections, each in turn subdivided into 14 plots of 22 rows each at 90 cm spacing. Twenty plants of each genetic material were planted per furrow in plots laid out in a completely randomized design. Tubers were planted 30cm apart along the row; an Alpha tuber was included in each row within each plot as a check. Whole plants, i.e., including both the aerial portion and all tubers, were sampled on September 10, 98 days after planting. On this single occasion three plants were collected from each row, one from either end, and one from the middle section of the row. Each whole plant collected was wrapped in aluminum foil, properly identified, frozen in liquid nitrogen and stored in the dark at -20 C until analyzed. All samples were processed within four weeks following sampling date.

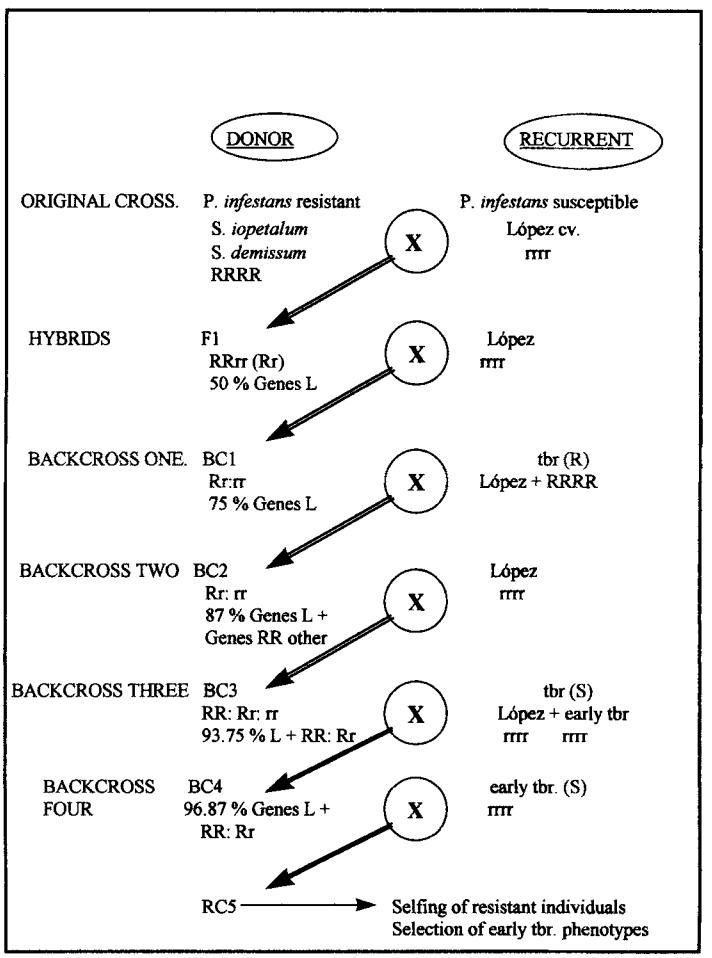


FIGURE 1.
Backcrossing scheme designed to obtain a *P. infestans*-resistant and early tuberizing potato cultivar.

Sample Analysis

Each sample for glycoalkaloid analysis consisted in 10 g of tuber tissue or 5 g of leaf tissue. At least three such samples were used for glycoalkaloid determination on each plant collected on the sampling day. Procedures for tuber extraction and separation of alkaloids by thin layer chromatography (TLC) have been described before (Coria *et al.* 1998). Foliage extraction procedure was the same as for tubers except that a double filtration step was practiced to minimize pigment interference. This filtration step was performed after evaporative concentration and before precipitation of the alkaloids with NH_4OH. Quantification of individual solanidine, α-chaconine, and α-solanine was performed on TLC plates previously developed with ceric ammonium sulphate by densitometry (MultiImage Light Cabinet Alpha Imager 2000 and AlphaEase image processing and analysis system, Alpha Innotech Corp. San Isidro, CA). High purity α-solanine, α-chaconine, and solanidine (Sigma Chemicals) were included in each TLC plate and calibration curves were obtained for each alkaloid run separately at different concentrations to obtain the final amount of each alkaloid in the samples by regression analysis. Linear regression analysis of these standard curves (data not shown) yielded r = 0.995, r = 0.993 and r = 0.979 as correlation coefficients for solanidine, α-solanine, and α-chaconine, respectively.

Non parametric late blight assessment was made by visual inspection of whole plants and sampled

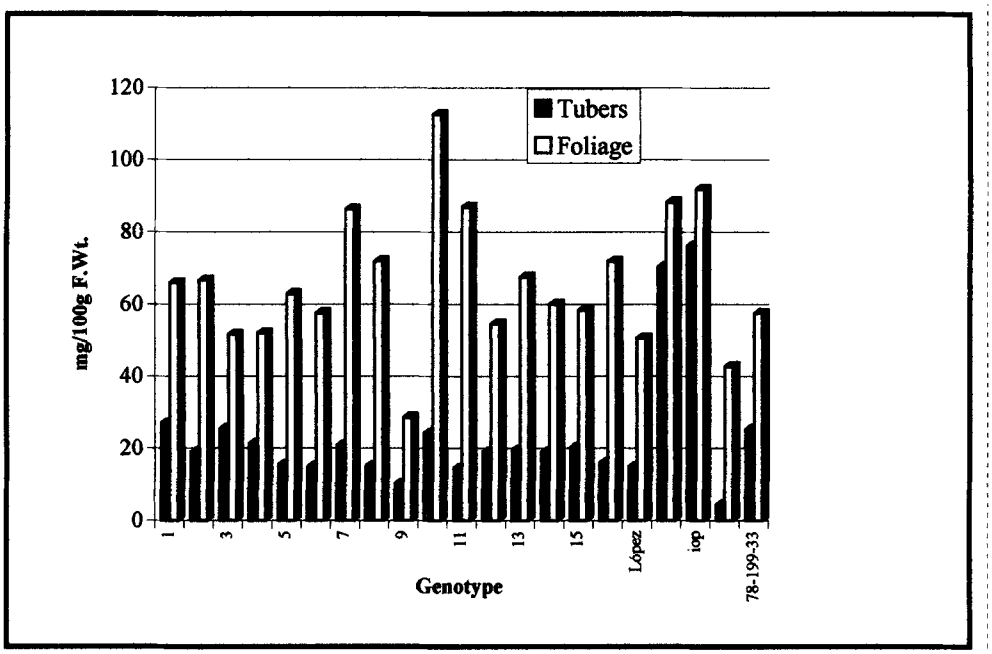
tubers cut in half. Extent of damage in both, foliage and tubers was described as either little, extensive, or total.

RESULTS AND DISCUSSION

Comparison of Total Alkaloid Content Between Foliage and Tuber Tissue

Using the corresponding standard curves, each alkaloid was quantified in leaf and tuber tissues from wild donors, advanced and commercial clones, as well as from hybrids from three cycles of backcrossing from a breeding program aimed at deriving new varieties with high levels of resistance to late blight.

Most studies have shown that the aerial portion of the potato plant synthesizes larger amounts of glycoalkaloids than the tubers (Phillips *et al.* 1996). Our own analysis showed significant differences in total glycoalkaloid content (TGA) between tubers and foliage. Furthermore, TGA content in the foliage was at least twice, but even more than three times as large as in the tubers of several of the materials tested (Figure 2). This large difference in TGA content between foliage and tubers has been attributed to the larger fluctuations in light intensity, humidity, and temperature around the aerial versus the underground portions of the developing plant (Jadhav and Salunkhe 1975; Woolfe 1987). Only a poor correlation (r = -0.477) was



Key to numbered genotypes in **Figure 2.**

1 E-91-64-1 BC-2 IOP	6 E-92-17-50 BC-3 IOP	11 E-94-8-10 BC-4 IOP
2. E-91-80-6 BC-2 dms	7 E-92-17-28 BC-3 dms	12 E-94-10-34 BC-4 iop
3 E-91-20 6 BC-2 iop	8 E-92-10-10 BC-3 dms	13 E-94-16-41 BC-4 iop
4 E-91-32-5 BC-2 dms	9 E-92-18-5 BC-3 iop	14 E-94-26-16 BC-4 dms
5 E-91-78-1 BC-2 iop	10 E-92-7-14 BC-3 iop	15 E-94-31-26 BC-4 iop

FIGURE 2.
Total glycoalkaloids in tubers and foliage of parentals and hybrids from various cycles of backcrossing designed to obtain a *P. infestans*-resistant and early tuberizing potato cultivar.

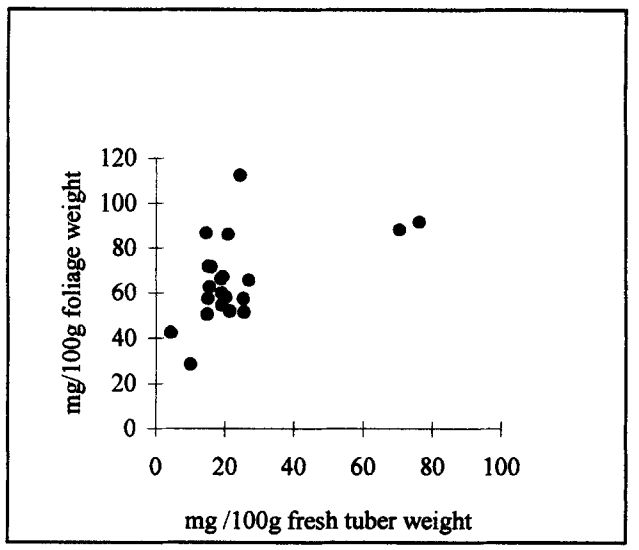


FIGURE 3.
Relation between total glycoalkaloid content in tubers and leaves from genetically related genotypes (r = -0.4768).

found between TGA content in the tubers and that in the foliage (Figure 3).

Tuber Alkaloids

Analysis of variance showed significant genotypic effect on TGA, α-solanine, α-chaconine, and solanidine content in both tubers and leaves (Table 2). All tubers sampled contained α-solanine and α-chaconine; solanidine, on the other hand, was detected only in tubers from Alpha, advanced clone 78-199-33, and hybrids E-91-32-5dms and E-91-78-1iop, from backcross cycle 2 (BC2); E-92-10-10dms, and E-92-18-5iop from backcross cycle 3 (BC3) (Table 3). In tubers solanidine appeared typically in very low amounts in comparison with the glycosylated forms and represented not more than 5% of TGA content, while α-solanine and α-chaconine represented 57% and 38% of TGA, respectively; van Gelder (1990) reported 95% α-solanine and α-chaconine in many *S. tuberosum* clones. α-Solanine was the single most abundant of the three alkaloids studied in most backcrosses, wild parentals, and the advanced clone, while E-92-18-5iop and Alpha had the largest amount of α-chaconine. TGA content was highest in *S. demissum* and *S. iopetalum*, 70.4 and 76.2 mg/100 g fresh weight, respectively. These values are more than three times the maxium permitted TGA. They are not, however, the highest reported in the literature: *S. vernei*, for example, a clone highly resistant to cyst nematode (*G. pallida* and *G. rostochiensis*) has been reported to accumulate up to 157 mg TGA/100 g fresh weight, and van Gelder (1990) has observed that such wild species are characterized by a greater probability to pass this trait onto their offspring. Table 3 also shows that commercial clones Alpha and Lopez had an average TGA content of 15.9 and 14.8 mg/100 g fresh weight, respectively, both below the limit for human consumption. These values agree well with previous reports using the same clones (Sinden 1987; Woolfe 1987). It is worth noting that being under fungicide protection, sampled tissues of Alpha did not show extensive damage by late blight.

TABLE 2.—*F ratios of mean squares to error mean squares from ANOVA performed on the effect of genotype on α-solanine, α-chaconine, and total glycoalkaloid content in tubers and leaves of 15 hybrids from a backcrossing breeding scheme aimed at obtaining a* P. infestans*-resistant and early tuberizing potato cultivar.*

Source of variation		F ratios		
	d.f.	α-solanine	α-chaconine	TGA
Genotype				
Tubers	14	8.62**	7.35**	12.07**
Foliage	14	3.04**	10.93**	3.76**

** Significant at the 0.01 level of probability.

Little is known about the inheritance of glycoalkaloid content in potato species. It has been proposed that this trait is polygenic and highly heritable (Sanford and Sinden 1972). Thus, any hybrid between a wild potato species and a commercial potato clone has a high probability of high TGA content.

Tuber TGA content among hybrids from all backcrossing groups averaged quite acceptable TGA levels (19 mg/100 g fresh weight). Although not statistically significant, hybrids in the BC2 group showed higher concentrations of TGA than hybrids from subsequent backcrosses, 21.6 vs 17.0 or 18.4 mg/100 g fresh weight in BC2, BC3, and BC4 groups, respectively. The BC2 group also contained a larger number of hybrids with TGA content above 20 mg/100 g fresh weight (Table 3). This probably resulted from using a different method to obtain BC2: instead of the conventional use of the simple recurrent recessive parent, in this case, the wild donor was used twice successively to generate the hybrid used to cross by RC1. In doing this, the probability increased for inheriting the genes that express high TGA content, while the

TABLE 3.—*Mean solanidine, α-chaconine, α-solanine, and total glycoalkaloid content in tubers of parentals and hybrids from four backcrossing cycles from a breeding scheme aimed at obtaining a* P. infestans*-resistant and early tuberizing potato cultivar.*

		(mg/100g fresh weight)			
Genotype	BC Group	Solanidine	α-Chaconine	α-Solanine	TGA
E-91-64-1iop	2	ND	11.4	15.4	26.9
E-91-80-6iop	2	ND	8.0	10.7	18.8
E-91-20-6iop	2	ND	10.0	15.5	25.5
E-91-32-5dms	2	2.3	5.6	13.4	21.3
E-91-78-1iop	2	1.2	6.5	7.6	15.3
E-92-17-50dms	3	ND	6.9	8.0	14.9
E-92-17-28dms	3	ND	7.7	13.1	20.8
E-92-10-10dms	3	2.5	2.6	9.9	15.1
E-92-18-5iop	3	2.6	5.3	2.0	10.1
E-92-7-14iop	3	2.6	10.0	13.3	24.2
E-94-8-10iop	4	ND	5.6	8.8	14.4
E-94-10-34iop	4	ND	5.5	13.4	19.0
E-94-16-41iop	4	ND	8.4	10.9	19.4
E-94-26-16dms	4	ND	6.2	12.7	19.0
E-94-31-26dms	4	ND	6.8	13.4	20.2
S. *demissum*		ND	36.4	34.0	70.4
S. *iopetalum*		ND	29.0	47.2	76.2
Alpha		3.8	6.3	5.8	15.9
Lopez		ND	4.6	10.1	14.8
IRERI		ND	2.0	2.3	4.3
78-199-33		4.2	6.5	14.4	25.5

$LSD_{(0.01)}$ = 2.7 (α-chaconine), 5.8 (α-solanine), and 9.1 (TGA).
ND = Not detected

commercial susceptible clone (Lopez) was used to cross by BC2 and BC3 in order to obtain backcrosses 3 and 4, respectively. As Fig. 1 shows, each BC2 material was backcrossed to the recurrent parent three times, including the Lopez x RRRR hybrid, and as this process continues, more of the genes of the recurrent parent accumulate.

The BC3 group included material with the lowest TGA content (E-92-18-5iop, 10.1 mg/100 g fresh weight). As Table 1 shows, the basic difference in pedigree between this material and the others in BC3 is that RC1 was not backcrossed to the resistant donor. This means that E-92-18-5iop has been crossed to the wild parent once only. It is also worth noting that this material did not show any detectable levels of α-solanine, which was the most abundant alkaloid in all hybrids. Thus, selection of hybrids in BC3 with high resistance to late blight, but low tuber TGA levels seems at hand.

The BC4 group of hybrids is characterized by almost 97% of the genes that belong to Alpha or Lopez (Table 1). Although of different pedigree, these hybrids showed similar low TGA content, as would be expected after continued backcrossing, the net result of which is homozigosity at an increasing number of loci, including those that express TGA content.

A significant difference in TGA content between the advanced clone and the variety tested was observed, with clone 78-199-33 showing a TGA almost six times greater than that of cv. IRERI, which had the lowest TGA content among all materials studied. TGA in clone 78-199-33 was similar to that in some of the hybrids in the BC2 group. Since such content exceeded 25 mg/100 g fresh weight, this clone would have to undergo one more backcross to the *tuberosum* parent to bring TGA levels below the safety limit.

From these data, it may be concluded that backcrossing seems to have been an important factor in reducing tuber TGA content in the materials analyzed. Continued selection for late blight resistance together with low TGA content and other tuber quality parameters may yield useful varieties from many of the materials analyzed here.

Foliage Alkaloids

S. demissum and *S. iopetalum* showed the highest TGA content in leaves (88.19 and 91.8 mg/100 g fresh weight, respectively). Table 4 lists individual and TGA content in leaves of all materials studied. Alpha and Lopez also registered high leaf TGA content (71.8 and 50.6 mg/100 g fresh weight, respectively). Solanidine was present in leaves of Alpha, Lopez, *S. demissum*, *S. iopetalum*, IRERI, clone 78-199-33, and some hybrids within backcrossing groups. Average solanidine content in these materials was 12.8% of TGA. This was more than twice the level found in tubers (5%). It is not known whether a higher solanidine synthesis rate in foliage than in tubers and/or a higher glycosylation rate in tubers than in foliage is responsible for this pattern. On the other hand, α-solanine and α-chaconine were present in all leaf samples. The concentrations of glycosylated forms constituted 87.2% of TGA present in foliage; 43.7% was found as α-solanine and 43.5% as α-chaconine.

The BC3 group had the highest average TGA content in foliage (71.3 mg/100 g fresh weight), while as we saw earlier, this group had the lowest average TGA content in tubers. In contrast, the BC2 group was higest in tuber TGA but lowest in foliage TGA content, 59.8 mg/100g fresh weight. However, this did not constitute a general pattern, as indicated by the fact that some materials had low TGA content in both tubers and leaves (E-92-18-5iop in BC3 and IRERI), while still others

TABLE 4.—*Mean solanidine, α-chaconine, α-solanine, and total glycoalkaloid content in leaves of parentals and hybrids from four backcrossing cycles from a breeding scheme aimed at obtaining a* P. infestans*-resistant and early tuberizing potato cultivar.*

		(mg/100g fresh weight)			
Genotype	BC Group	Solanidine	α-Chaconine	α-Solanine	TGA
E-91-64-1iop	2	ND	32.1	33.7	65.9
E-91-80-6iop	2	8.8	36.4	21.4	66.6
E-91-20-6iop	2	6.0	24.1	21.5	51.6
E-91-32-5dms	2	13.0	19.6	19.3	52.0
E-91-78-1iop	2	ND	24.7	38.2	62.9
E-92-17-50dms	3	ND	23.6	34.0	57.6
E-92-17-28dms	3	5.1	39.1	42.1	86.2
E-92-10-10dms	3	ND	32.8	39.4	71.9
E-92-18-5iop	3	4.0	14.2	10.2	28.5
E-92-7-14iop	3	40.0	43.3	29.2	112.5
E-94-8-10iop	4	13.0	29.1	44.6	86.8
E-94-10-34iop	4	ND	27.4	27.1	54.5
E-94-16-41iop	4	3.0	33.9	30.6	67.5
E-94-26-16dms	4	12.6	18.3	29.1	60.0
E-94-31-26dms	4	6.2	21.7	30.4	58.3
S. *demissum*		18.8	27.7	41.7	88.2
S. *iopetalum*		29.9	35.0	26.9	91.8
Alpha		8.9	30.8	34.9	71.8
Lopez		17.2	21.9	11.5	50.6
IRERI		1.5	26.3	15.5	42.7
78-199-33		3.2	29.6	24.7	57.5

$LSD_{(0.01)}$ = 11.8(α-chaconine), 12.4 (α-solanine), and 21.0 (TGA).
ND = Not detected

had high TGA content in both tissues (*S. demissum* and *S. iopetalum*, E-91-64-1iop in BC2, and clone 78-199-33). Although the relationship between TGA content in foliage and in tubers is not clear, it seems possible to select materials that have low TGA content in tubers and high TGA in leaves. As has been suggested, this selection would be convenient if glycoalkaloids contribute to protection against pathogens and pests that attack the aerial portion of the plant (Sinden *et al.* 1984).

In contrast to the case of tuber tissue, backcrossing did not seem to influence TGA content in foliage. Tubers from backcrosses had 65.3% less TGA than either wild species used as parents, while foliage TGA content in backcrosses was only 15% lower than in parents. TGA content in leaves of Alpha and Lopez was relatively high (71.8 and 50.6 mg/100 g fresh tissue, respectively). Since *S. demissum* and *S. iopetalum* also showed high foliage TGA content (88.2 and 91.8 mg/100 g fresh tissue, respectively), it can be expected that backcrosess would be rich in foliage alkaloids, as was the case.

Total TGA Content and Resistance to Late Blight

Ambient conditions in the Toluca Valley during the crop cycle in this experiment were conductive to a high incidence of late blight, yet simple visual inspection allowed confirmation that backcrosses resisted infection well. Foliage in each backcross showed only small lesions which did not affect tuber production. Late blight resistance among backcrosses was remarkable: 100% survival was observed and an acceptable number of commercial tubers per plant (six in average, larger than 4.0cm in length) were harvested. In contrast, check Alpha plants within the same rows as the hybrids and wild species–and thus, left unprotected by fungicide spraying for the duration of the crop cycle–were severely affected by the disease, as in this case foliage showed extensive and severe lesions, which ultimately led to plant senescence and death. As long as ambient conditions allow, late blight will inhibit tuber production, as observed in Alpha.

As has been noted, tubers can also be infected by late blight. In this experiment, in spite of a heavy innoculum pressure in the fields of the experimental station, tubers from backcrosses were not affected by the disease, while tubers from the susceptible cultivars appeared severely damaged. The resistance to late blight within each backcross varied, but all compared better with *S. demissum* and *S. iopetalum* than with the commercial parental clones with regard to the extent of infection.

According to the field resistance observed and the relatively low TGA content in tubers, it appears there was no relation between high tuber TGA content and resistance to *P. infestans*. Early work by Shih and Kuc (1973) showed that the accumulation of glycoalkaloids in mechanically damaged potato tubers was inhibited in the presence of *P. infestans*, which induced the synthesis of the phytoalexin reshitine.

Similar results have been observed in studies with *P. infestans*, *Fusarium*, and *Phoma* that concluded there was no relation between resistance and tuber TGA content, as some genotypes that were resistant to these pathogens were lower in TGA than the more susceptible ones (Olsson 1987).

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