Diversity of Sesquiterpenes in 46 Potato Cultivars and Breeding Selections

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Rishitin, lubimin, and solavetivone were the major sesquiterpenes found in 46 cultivars and breeding selections of potato (*Solanum tuberosum* L.). Concentrations of total sesquiterpenes were low or undetectable in untreated tuber slices, but ranged from 5 to 101 μg/g of fresh weight 4 days after treatment with the elicitor arachidonic acid. Seven genotypes produced significantly ($P < 0.01$) higher sesquiterpene concentrations than Russet Burbank (17 μg/g), a widely grown commercial cultivar. More than half of the genotypes tested were significantly ($P < 0.01$) different from Russet Burbank in sesquiterpene composition due to higher ratios of lubimin or solavetivone, both of which are reported to be biosynthetic precursors of rishitin. The highest ratios of solavetivone to total sesquiterpenes were strongly correlated with derivation from *S. tuberosum* ssp. *andigena* CPC 1673, which confers the H1 gene for resistance to the golden nematode (*Globodera rostochiensis*).

Keywords: *Solanum tuberosum; potato breeding; sesquiterpenes; Globodera rostochiensis*

INTRODUCTION

The potato (*Solanum tuberosum* L.) is the fourth most important food crop in the world and the most important vegetable crop in the United States (Spooner and Bamburg, 1994). The cultivated potato (*S. tuberosum* ssp. *tuberosum*) originated in South America, where a wide variety of primitive cultivars and wild species relatives still exist. Many wild potato species are genetically interfertile with the cultivated potato, and some wild species are highly resistant to important potato pathogens (Plaisted and Hoopes, 1989; Ross, 1986; Spooner and Bamberg, 1994). Despite the availability of such disease-resistant germplasm, potato disease control has traditionally relied heavily on the use of chemical pesticides, making potatoes the most heavily chemically treated major crop (Spooner and Bamberg, 1994).

Increased public concern about pesticide use on food crops and the recent emergence of pesticide-resistant strains of several important pathogens (Deahl et al., 1993; Desjardins et al., 1993; Kawchuck et al., 1994) have stimulated ongoing efforts to develop cultivars with enhanced disease resistance by incorporating germplasm from wild potato species. This approach, however, is not without its pitfalls. Wild plants may owe their disease resistance to higher levels of toxic chemicals than are found in their cultivated relatives (Ames et al., 1990). Consequently, potato breeders should anticipate that since selection for increased disease resistance may also select for these natural toxins, a thorough biochemical screening of new cultivars may be advisable.

Cultivated potato tubers contain low levels of a number of chemically diverse toxins and potential toxins. These include glycoalkaloids, various phenols, and a large family of sesquiterpenes including norsesquiterpenes (Figure 1) (Kuc, 1982). Much of the research on the biochemistry of fungal disease resistance in potato tubers has focused on the sesquiterpenes, because they are fungitoxic in vitro and they can accumulate to high levels near infection sites. In addition, no harmful effects have been observed following limited testing on mice (Brishammer, 1987) and chicken embryos (Wood, 1976), which suggests that at least some sesquiterpenes may present a low risk of toxicity to humans. More than 20 sesquiterpenes have been isolated and characterized from potatoes (Kuc, 1982); most of these studies have used Kennebec and Russet Burbank, which are widely grown commercial cultivars (Bostock et al., 1981; Rohwer et al., 1987; Zook and Kuc, 1991). Rishitin and lubimin have consistently been the major sesquiterpenes identified in tubers of cultivars Kennebec and Russet Burbank after treatment with a variety of pathogens or with arachidonic acid, a fungal cell-wall lipid that is a strong elicitor of potato sesquiterpenes (Bostock et al., 1981).

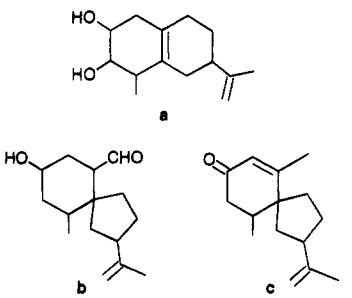

Figure 1. Structures of rishitin (a), lubimin (b), and solavetivone (c).

The primary objective of our study was to investigate the sesquiterpenes of a diverse collection of 46 potato cultivars and breeding selections, many of which incorporate germplasm from primitive cultivars and wild potato species. We examined tuber sesquiterpene composition and concentration both before and after treatment with arachidonic acid. We also looked for correlations between sesquiterpene contents and tuber resistance to the golden nematode (*Globodera rostochiensis*) and to dry rot (*Fusarium sambucinum*).

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Table 1. Commercial Potato Cultivars Evaluated in this Study

name	release date[a]	dry rot reaction[b]	name	release date[a]	dry rot reaction[b]
Atlantic	1978	S-VS	Lemhi Russet	1981	S
BelRus	1978	MR-MS	Lenape	1967	S
Butte	1978	S	Monona	1964	S
Century Russet	1995	S	Nooksack	1973	S
Cherokee	1951	R-MR	Norchip	1968	MS-S
Chipeta	1993	S	Norgold Russet	1964	S-VS
Desiree	1962	MS-S	Norking Russet	1985	MS-S
Frontier Russet	1990	R-MR	Norland	1957	MS-S
Gemchip	1989	MR-MS	Ranger Russet	1991	MR-MS
Goldrush	1992	MR-MS	Red LaSoda	1953	MR-MS
Genesee	1993	NT	Rosa	1981	MS-S
Hilite	1987	R-MR	Russet Burbank	before 1910	S
Kanona	1988	NT	Russet Norkotah	1988	MR-MS
Katahdin	1932	S	Shepody	1980	S
Kennebec	1948	S	Wauseon	1967	MS
Krantz	1985	MR-MS			

[a] Data on date of release are from the Potato Pedigree Management database developed by Steve Love, University of Idaho, Aberdeen Research and Extension Center, Aberdeen, ID. [b] Data on tuber dry rot reaction are from tests performed as described in Corsini and Pavek (1986) on tubers grown at the University of Idaho Research and Extension Center, Aberdeen, ID, except for Cherokee (G. W. Ayers, Canada Department of Agriculture, Charlottetown, PE, Canada), Wauseon (S. Leach, University of Maine, Orono, ME), and Desiree (M. J. Adams, Rothamsted Experimental Station, Harpenden, Herts., U.K.). R, resistant; MR, moderately resistant; MS, moderately susceptible; S, susceptible; VS, very susceptible; NT, not tested.

MATERIALS AND METHODS

Potatoes. Genotypes Cherokee, PI 205624, USDA x96-56, USDA s41956, Wauseon and B0172-22 were kindly supplied by K. G. Haynes, USDA-ARS, Beltsville, MD. Genotypes Genesee, Kanona, NY103, and NY11-45 were kindly supplied by R. Plaisted, Plant Breeding Department, Cornell University, Ithaca, NY. All other cultivars and breeding selections were obtained from USDA-ARS, University of Idaho, Aberdeen, ID. Tubers were stored at 8 °C and brought to room temperature 1 day before testing.

Sesquiterpene Elicitation. Sesquiterpenes were elicited in potato tuber slices by a modification of published methods (Bostock et al., 1981). Tuber slices (0.5–0.8 cm thick and 3 cm in diameter) were prepared aseptically from the medullary tissue of each of the test potatoes. Ten slices were placed in a 15 cm plastic Petri dish lined with moist filter paper. The Petri dishes were placed in plastic bags, and the slices were aged for 1 day at 18 ± 1 °C. Each slice was then spread with 100 μL of absolute ethanol with or without 20 mM arachidonic acid (Sigma Chemical Co.). The Petri dishes were returned to plastic bags and incubated at 18 ± 1 °C for 4 more days. The cultivar Russet Burbank was included as a control with every group of potatoes tested.

Sesquiterpene Analysis. Ten untreated or 30 treated tuber slices for each cultivar were weighed, and then each slice was cut into three parts. The combined pieces from each treatment were extracted overnight with 300 mL of diethyl ether, and the extracts were concentrated on a rotoevaporator. The concentrate was redissolved in 100 mL of diethyl ether, filtered through a pad of anhydrous sodium sulfate, and concentrated to dryness. The residue was redissolved in 5 mL of ethyl acetate, and sesquiterpenes were analyzed by gas–liquid chromatography (GLC) with flame ionization detection on a gas chromatograph (Hewlett-Packard 5890, Palo Alto, CA) fitted with a 30 m DB-1 column. The column was held at 120 °C at sample injection and then heated to 210 °C at 15 °C/min and held at for 4 min. The column was then heated to 260 °C at 15 °C/min and held 2 min. Under these conditions, the metabolites had the following retention times: solavetivone, 5.8 min; rishitin, 6.0 min; and lubimin, 8.5 min. Compound identifications were confirmed by GC–MS recorded on a Hewlett-Packard 5891 fitted with a DB-5MS column and the source operated at 1800 eV. The column was temperature programmed from 120 to 210 °C at 15 °C/min and then held for 3 min; injection temperature was 250 °C. The sesquiterpene detection limit was equivalent to 0.5–1.0 μg/g of tuber fresh weight.

The concentrations of the sesquiterpenes in each extract were determined by standard curves of rishitin, lubimin, and solavetivone prepared from arachidonic acid-treated tubers of potato cultivars as described previously (Desjardins et al., 1989). Treated slices of potato were extracted overnight with diethyl ether. The extracts were filtered through anhydrous sodium sulfate. The pooled extracts were concentrated under reduced pressure. Crude extracts were initially separated on silica gel columns (dichloromethane/MeOH 19:1). Fractions were checked by TLC and GLC; fractions containing solavetivone, lubimin, or rishitin were combined. A second purification was done on silica gel column in ether/hexane (4:1) for solavetivone, in ether/hexane (9:1) for lubimin, and in ether/methanol (19:1) for rishitin. A final purification with hexane/2-propanol (5:1) removed butylated hydroxytoluene (BHT). Identifications of purified compounds were confirmed by GC–MS, ^{1}H NMR, and ^{13}C NMR.

Evaluation of *Fusarium* Dry Rot Reaction. Evaluations of *Fusarium* dry rot reaction were conducted as described by Corsini and Pavek (1986). Tubers of cultivars and breeding selections were grown under typical field conditions at the University of Idaho Research and Extension Center, Aberdeen, ID. Evaluations were made 10–12 weeks following tuber inoculation and incubation at 10 °C. The numerical rot index was converted to a resistance designation for comparison with evaluations reported by others: 1 = no rot, the pathogen was completely contained (resistant, R); 2 = slight spread of rot from the inoculation site but the pathogen appeared to be contained (resistant to moderately resistant, MR); 3 = rot involving about 5–25% of the exposed surface in the region of the inoculation site, pathogen was restricted but not contained (moderately susceptible, MS); 4 = active rot involving 25–75% of the exposed surface in the region of the inoculation site (susceptible, S); 5 = active rot involving >75% of the tuber (very susceptible, VS). Dry rot data were available for 36 of the 46 potato genotypes in this study.

RESULTS AND DISCUSSION

Selection of Potato Genotypes for Testing. Potato genotypes for testing were selected to include well-established commercially grown cultivars as well as a wide variety of newer cultivars and breeding selections that incorporate germplasm from wild species and from primitive cultivars of *S. tuberosum* (Tables 1 and 2). Russet Burbank was chosen as a control for all experiments because it is the most widely grown cultivar in the United States and because this 100-year-old cultivar (and its parent, Early Rose) have contributed heavily to the pedigrees of essentially all commercial cultivars grown in the United States (Plaisted and Hoopes, 1989). Russet Burbank is a long, russet-skinned potato with

Table 2. Potato Breeding Lines Evaluated in This Study

no.	selected exotic germplasm in pedigree (F1–F5)[a]	dry rot reaction[b]
A75379-3	*S. tuberosum* ssp. *andigena* (F5)	R-MR
A69868	*S. tuberosum* ssp. *andigena* (F4)	R-MR
ATD63-7	*S. microdentum* (F1)	R-MR
B0172-22	*S. chacoense* (F5), *S. demissum* (F4)	R
BR6316-7	*S. chacoense* (F4), *S. tuberosum* ssp. *andigena* (F4)	R-MR
JHA4711	*S. brevidens* (F2)	NT
NYE11-45	*S. tuberosum* ssp. *andigena* (F2 and F5)	NT
NY103	*S. tuberosum* ssp. *andigena* (F5)	NT
NYR247-1	*S. tuberosum* ssp. *andigena* (F1)	NT
PA89A03-4	*S. chacoense* (F2)	NT
PA89A18-19	*S. chacoense* (F2)	NT
PI205624	*S. tuberosum* ssp. *andigena* (F1)	R
USDA x96-56	*S. demissum* (F2)	NT
USDA s41956	*S. tuberosum* ssp. *tuberosum* from Chile (F2)	NT
WN245-2	*S. demissum* (F4)	R-MR

[a] Pedigree data as in Table 1 footnote *a*. Additional information was supplied by K. L. Haynes and R. L Plaisted. [b] Dry rot reaction data are as in Table 1 footnote *b*, except for B0172-22 and PI205624 (K. L. Haynes).

excellent baking and processing quality. Other widely grown, long, russet-skinned cultivars tested in this study include Belrus, Frontier Russet, Hilite, Lemhi Russet, Nooksack, Norgold, Norking Russet, Russet Norkotah, and Ranger Russet. Katahdin (released in 1932) and its progeny Kennebec (released in 1948) are standard round, smooth-skinned potato cultivars widely grown for fresh use and processing. These two cultivars have also contributed heavily to the pedigrees of modern North American cultivars (Plaisted and Hoopes, 1989). Other commercially important, smooth-skinned cultivars tested in this study include Gemchip, Norchip, and Shepody, and the red-skinned cultivars Norland and Red LaSoda. Other recently released commercial cultivars were selected for testing because they contain a significant percent of germplasm from primitive cultivars and wild potato species. For example, primitive cultivars of *S. tuberosum* ssp. *andigena* contribute to the pedigrees of cultivars Atlantic, Genesee, Kanona, Rosa, and Wauseon. The primitive cultivar *S. phureja* is a great-grandparent of cultivar Krantz. The wild potato species *S. chacoense* and *S. demissum* are great-grandparents of cultivars Lenape and Cherokee, respectively. Most of the 15 potato breeding selections were chosen for testing because they were prominent in the parentage of commercial varieties tested or because they incorporated particularly high levels of exotic germplasm. Some genotypes were selected because they were reported to show high levels of resistance to *G. rostochiensis* or to *F. sambucinum*.

Sesquiterpenes in Control Potato Tubers. Potato tuber slices that were freshly cut, aged for 24 h, or incubated for 4 days after treatment with ethanol without arachidonic acid accumulated very low or undetectable amounts of sesquiterpenes (Figure 1). For example, tuber slices of 19 genotypes were analyzed for sesquiterpenes 4 days after treatment with ethanol. Seven genotypes (ATD63-7, BR6316-7, Desiree, Frontier Russet, Gemchip, Red LaSoda, and WN245-2) produced no detectable sesquiterpenes. Cultivar Monona produced rishitin at 3 μg/g of tuber slice fresh weight; Chipeta produced lubimin, 0.5 μg/g; Russet Burbank produced both rishitin and lubimin, total 3 μg/g. Genotypes A69868, Nooksack, PA89A03-4, PA89A18-19, and Rosa produced solavetivone, 0.3–3 μg/g; Krantz produced rishitin and solavetivone, total 4 μg/g; Norland produced solavetivone and lubimin, total 0.7 μg/g; Goldrush and Katahdin produced all three sesquiterpenes, total 2–4 μg/g. These results are consistent with previous reports that sesquiterpene concentrations are low in control tubers, including genotypes BR6316-7, Katahdin, Kennebec, and Russet Burbank (Bostock et al., 1981; Corsini and Pavek, 1980; Osman and Moreau, 1985; Zook and Kuc, 1991) and four German cultivars (Rohwer et al., 1987).

Table 3. Sesquiterpene Production by Potato Genotypes after Treatment with Arachidonic Acid[a]

name/no.	total sesquiterpenes (μg/g)	solavetivone (μg/g)	lubimin (μg/g)	rishitin (μg/g)
Rosa	104	101	1	2
PA89A03-4	78	21	38	19
USDA x96-56[b]	52	13	33	6
Genesee	50	45	1	4
Butte	43	0	41	1
Norgold	42	0	41	1
Chipeta	40	10	27	3
Nooksack	36	21	10	5
B0172-22[b]	34	18	4	12
Cherokee[b]	33	19	2	12
PI205624[b]	32	24	1	7
Kanona	27	23	2	2
Norking Russet	26	4	14	7
Goldrush	25	7	15	4
Katahdin	25	3	14	8
WN245-2	25	4	9	12
Kennebec	24	4	16	4
NYE11-45	22	17	3	2
BR6316-7	21	19	1	1
Wauseon[b]	21	18	1	2
A69868-2	19	16	1	2
Red LaSoda	18	78	9	1
Krantz	18	8	4	7
HiLite	18	13	4	1
Russet Burbank[c]	17	2	9	6
JHA4711	17	2	9	6
NY103	16	8	6	2
USDA s41956[b]	15	4	6	5
PA89A18-19	15	9	3	3
Desiree	14	5	4	5
NYR247-1	14	4	4	6
A75379-3	14	10	1	3
Ranger Russet	14	2	12	0
Norchip	13	4	6	3
Lenape	11	2	6	3
Norland	11	1	8	2
Lemhi Russet	11	2	9	0
Atlantic	10	8	2	0
ATD63-7	10	1	4	5
Century Russet	10	3	5	2
Gemchip	9	4	2	3
Monona	8	2	2	4
Russet Norkotah	8	1	7	0
Shepody	6	1	3	2
Frontier Russet	5	3	2	1
Belrus	5	2	3	0

[a] Genotypes are listed in decreasing order of sesquiterpene concentration. Concentration and composition of sesquiterpenes (rishitin plus lubimin plus solavetivone) in arachidonic acid-treated potato tubers were assayed as described under Materials and Methods. Results are average of two experiments except where indicated. [b] One trial. [c] Result is average of 11 trials.

Sesquiterpenes in Arachidonic Acid-Treated Potato Tubers. Tuber slices of all 46 potato genotypes tested accumulated sesquiterpenes 4 days after treatment with 20 mM arachidonic acid (Table 3). This incubation time and similarly high concentrations of arachidonic acid have previously been shown to yield maximum sesquiterpene levels in various cultivars (Rohwer et al., 1987; Zook and Kuc, 1991). To test the reproducibility of sesquiterpene production, tubers of cultivar Russet Burbank were analyzed for sesquiter-

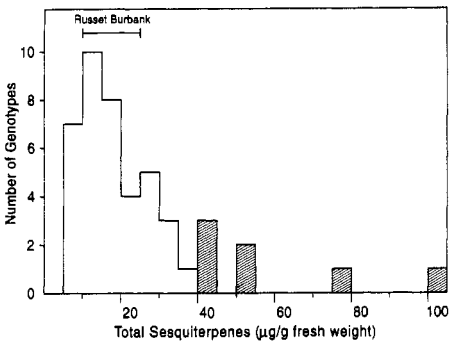

Figure 2. Frequency distribution histograms of the average concentrations of total sesquiterpenes (rishitin plus lubimin plus solavetivone) (micrograms per gram of potato fresh weight) for 45 potato genotypes compared to the control cultivar Russet Burbank tested at the same time (mean ± SD, $n = 11$). Genotypes indicated by hatchmarks differ significantly ($P < 0.01$) from Russet Burbank by Dunnet's t-test.

penes in 11 independent tests that extended throughout the duration of this study. In every test, rishitin and lubimin were the major sesquiterpenes detected, and solavetivone was a minor component. The concentration of total sesquiterpenes (rishitin plus lubimin plus solavetivone on a weight basis) varied from test to test; the mean and standard deviation were 17.2 ± 6.9 μg/g of tuber fresh weight, with a coefficient of variation of 40%. Relative yields by weight of the three sesquiterpenes were more consistent from test to test: rishitin, 35 ± 11%; lubimin, 52 ± 12%; and solavetivone, 12 ± 5% (means and standard deviations). All of the cultivars and breeding lines were tested twice, except for six (Cherokee, PI205624, USDA x96-56, USDA s41956, Wauseon, and B0172-22) which were tested only once because limited material was available. For statistical analysis, all treatments were compared by Dunnett's t-test (Sokal and Rohlf, 1969) to the Russet Burbank control tested at the same time.

Among all of the potatoes tested, the major sesquiterpenes produced were rishitin, lubimin, and solavetivone. Other potato sesquiterpenes were either not detected or were present at very low concentrations (<0.5 μg/g). Thirty-eight of the 45 genotypes did not produce significantly ($P < 0.01$) higher levels of total sesquiterpenes than cultivar Russet Burbank (Table 3 and Figure 2). Seven genotypes did show significantly increased levels of sesquiterpenes: in decreasing order, Rosa, PA89A03-4, USDA x96-56, Genesee, Butte, Norgold, and Chipeta. These high sesquiterpene producers are a genetically diverse group that incorporates unusually high levels of germplasm from primitive and wild potato species. The cultivar Rosa was the highest sesquiterpene producer, at 104 μg/g of fresh weight, which is more than 6 times the average yield from Russet Burbank. Rosa is an F1 hybrid between Wauseon, which is 12.5% group *andigena*, and an additional group *andigena* introduction. Genesee (50 μg/g) is an F2 descendent of Wauseon. In the development of cultivars Wauseon, Rosa, and Genesee, group *andigena* germplasm was used as the source of resistance to *G. rostochiensis*. It is clear, however, that incorporation of germplasm from group *andigena* does not always lead to high levels of sesquiterpenes, because Rosa's parent Wauseon and its F1 descendent NYE11-45 produce only 20 μg/g sesquiterpenes.

Wild potato species germplasm occurs among several of the high sesquiterpene producers. For example, breeding selection USDA x96-56 (52 μg/g) is an F2

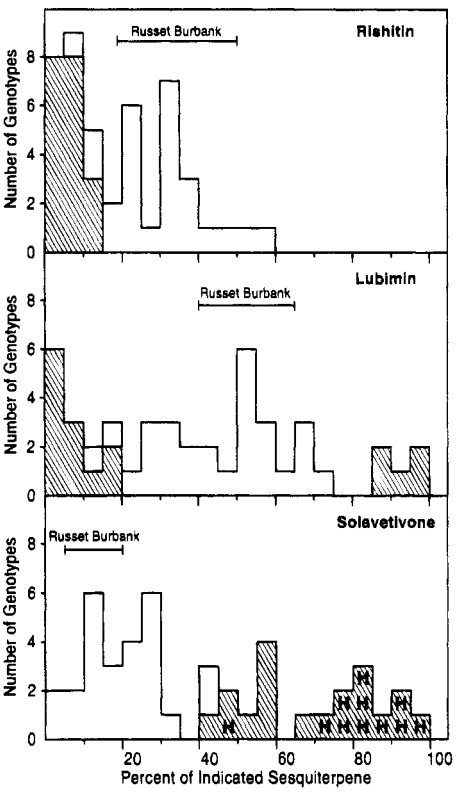

Figure 3. Frequency distribution histograms of the percent of each sesquiterpene (rishitin or lubimin or solavetivone) for 45 genotypes compared to the control cultivar Russet Burbank tested at the same time (mean ± SD, $n = 11$). Genotypes indicated by hatchmarks differ significantly ($P < 0.01$) from Russet Burbank by Dunnet's t-test. H designates genotypes derived from cultivar CPC1673.

descendent of *S. demissum*, which has had great impact as a source of resistance to late blight (17,19), but neither of its F1 descendents Cherokee (33 μg/g) or Kennebec (24 μg/g) was a high sesquiterpene producer. Breeding selection PA89A03-4 (78 μg/g) is an F2 descendent of S. *chacoense*, a source of resistance to potato leafroll virus. Chipeta (40 μg/g) also is a descendent (F6) of *S. chacoense*, but its grandparent Lenape produces only 11 μg/g sesquiterpenes. On the other hand, Norgold and its F1 descendent Butte are indistinguishable in both sesquiterpene levels (42–43 μg/g) and composition (see below). It must be emphasized at this point that all potato breeding is complicated by the fact that cultivated potatoes are tetraploid and inheritance of many genotypes is complex.

The seven genotypes that produced significantly higher levels of sesquiterpenes than Russet Burbank were also diverse in sesquiterpene composition (Table 3 and Figure 3). Genotypes Chipeta, PA89A03-4, and USDA x96-56 produced increased levels of all three sesquiterpenes in approximately the same proportion as Russet Burbank. The other four genotypes produced little or no rishitin. Butte and Norgold produced 96% lubimin, and Rosa and Genesee produced 88–98% solavetivone.

Five of the 46 genotypes tested produced very high (85%) ratios of lubimin (Table 3 and Figure 3). In addition to Norgold and its F1 descendent Butte, this group included Lemhi Russet, Ranger Russet, and Russet Norkotah, all of which are F2 descendents of Norgold. Norgold was developed for a high degree of resistance to common scab and was released in 1964. Although the trait for high lubimin production appears

Table 4. Sesquiterpene Production and Lineages of Potato Genotypes Derived from *S. tuberosum* Ssp. *andigena* CPC1673

	sesquiterpenes[a]		lineage to cultivar CPC 1673[b]					
name/no.	total μg/g	% solavetivone	F1	F2	F3	F4	F5	F6
PI205624	24	75	CPC1673					
Wauseon	18	89	B5149-8	1376-6	CPC1673			
Atlantic	8	83	Wauseon	B5149-8	1376-6	CPC1673		
BR6316-7	19	92	Wauseon	B5149-8	1376-6	CPC1673		
Rosa	101	98	Wauseon	B5149-8	1376-6	CPC1673		
Kanona	22	82	Peconic	LNA-106	1392-7	CPC1673		
A75379-3	10	74	A69868-2	Wauseon	B5149-8	1376-6	CPC1673	
Genesee	44	90	M348-45	Wauseon	B5149-8	1376-6	CPC1673	
NYE11-45	18	78	Rosa	Wauseon	B5149-8	1376-6	CPC1673	
NY103	8	49	Steuben	F9-31	B4494-3	B3944-1	PI205624	CPC1673

[a] Concentration and composition of sesquiterpenes (rishitin plus lubimin plus solavetivone) in arachidonic acid-treated potato tubers were assayed as described under Materials and Methods. Under the test conditions, Russet Burbank tubers produced an average of 17 μg/g total sesquiterpenes and 12% solavetivone. [b] Potato pedigree data are as in Table 1 footnote *a*. Additional information was supplied by K. L. Haynes and R. L. Plaisted.

to be derived from Norgold, it has not been possible to trace this phenotype back to a particular germplasm introduction. Norgold has a complex pedigree that is dominated by the cultivars Russet Burbank and Katahdin, neither of which produces an unusually high ratio of lubimin.

Sesquiterpenes and Resistance to *G. rostochiensis*. It has been possible to trace the high (75–98%) solavetivone ratios of 10 genotypes and the moderately high (49%) ratio of NY103 (Table 3 and Figure 3) to one germplasm introduction, a primitive Bolivian cultivar, *S. tuberosum* ssp. *andigena* CPC1673. Although tubers of CPC1673 could not be obtained to determine its pattern of sesquiterpene production, it is the likely source of high solavetivone ratios because CPC1673 is the only common ancestor of the cultivars Atlantic, Genesee, Kanona, Rosa, and Wauseon and the breeding selections A69868-2, A75379-3, BR6316-7, E11-45, NY103, and PI205624 (Table 4). Cultivar CPC1673 was identified in 1948 as a source of resistance to *G. rostochiensis* (Ellenby, 1952). Although its biochemical basis is not known, nematode resistance is due to a single dominant gene, designated H1, which has recently been mapped on potato chromosome V (Gebhardt, 1994; Pineda et al., 1993). All 11 descendents of CPC1673 that were tested in this study had previously been selected for cyst nematode resistance. The cosegregation of high solavetivone ratios with the H1 gene through several generations of outcrossing was unexpected. If this correlation is not simple coincidence, then solavetivone production might be involved in H1 mediated resistance. Although solavetivone does not appear to have been tested, rishitin was repellent and toxic to two nematode species in vitro and decreased nematode infection of the roots of pot-grown petunias (Alphey et al., 1988).

It is also possible that loci controlling sesquiterpene production are linked to the H1 locus on potato chromosome V. This hypothesis can be tested by analyzing segregating F1 progeny of crosses between suitable parental lines that differ in nematode resistance and solavetivone production. It is intriguing that chromosome V is the site of a number of resistance genes, including a locus for resistance to potato virus X, the R1 locus for race-specific resistance to late blight, and a region of quantitative resistance to late blight (Gebhardt, 1994).

Although the highest ratios of solavetivone were correlated with the H1 gene, six additional nematode-susceptible genotypes produced moderately high (50–70%) ratios of solavetivone (Table 3 and Figure 3). This group was genetically diverse and included cultivar Nooksack and its F2 descendent Frontier Russet, cultivar Hilite and its F2 descendent PA89A18-19, cultivar Cherokee, an F1 descendent of USDA x96-56, and B0172-22, a descendent of Monona and Lenape. The pedigrees of these genotypes did not identify any unambiguous source of these moderately high solavetivone ratios.

Sesquiterpenes and Resistance to *F. sambucinum*. Genetic analysis has shown that the ability of *F. sambucinum* strains to cause tuber dry rot is correlated with their ability to detoxify rishitin and lubimin in vitro (Desjardins et al., 1992). These results indirectly support a role for sesquiterpenes in potato tuber resistance to dry rot. If this is so, then potato genotypes that produce higher levels of sesquiterpenes may be more resistant to dry rot. To test this hypothesis, we compared the dry rot reaction data that were available for 34 genotypes (Table 1) to their sesquiterpene concentrations after treatment with arachidonic acid. There were no obvious correlations between dry rot resistance and total sesquiterpene concentrations or concentrations of individual sesquiterpenes. For example, cultivars Rosa and Norgold produced high levels of sesquiterpenes but were susceptible to dry rot, and Frontier Russet and ATD63-7 produced low levels of sesquiterpenes but were moderately resistant.

Conclusions. During the past three decades there has been a significant increase in genetic diversity of cultivars available to potato growers in North America. This change has resulted in large part from the incorporation of germplasm from primitive cultivars and wild species into a relatively narrow genetic base. The present study has shown that many newer potato cultivars and breeding selections differ from older cultivars in sesquiterpene concentration and composition, although there has been no deliberate selection for these traits per se. The major change we observed in this study was the accumulation of lubimin and solavetivone instead of rishitin. Current data indicate that solavetivone is a biosynthetic precursor of lubimin and that lubimin is a biosynthetic precursor of rishitin (Brindle et al., 1988; Murai et al., 1982). Therefore, accumulation of these earlier biosynthetic intermediates suggests that the last steps of the rishitin biosynthetic pathway may be suppressed in many of the newer cultivars.

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