The Germplasm Release of F87084, A Fertile, Adapted Clone With Multiple Disease Resistances

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ABSTRACT

F87084 is a germplasm release that has been developed by conventional breeding methods and can be traced back to very diverse germplasm sources. This clone has excellent female fertility, round-oval tubers and is well adapted to Eastern Canada. The vine maturity is slightly later than that of Kennebec, and the mean marketable yield is 78% of Kennebec. The specific gravity, boil, bake and chip scores are somewhat lower than Kennebec. F87084 is resistant to late blight, *Verticillium dahliae,* early blight, and the pathotypes of wart occurring in Newfoundland. F87084 has extreme resistance to PVY^{O} and PVX. It is also resistant to the potato cyst nematode pathotype Ro1. Progeny analyses indicate that F87084 is duplex for the genes controlling extreme resistance to PVX as well as resistance to the potato cyst nematode (Ro1).

RESUMEN

F87084 es un germoplasma liberado, que ha sido desarrollado con métodos convencionales de mejoramiento y que puede ser referido a muy diversas fuentes de germoplasma. Este clon tiene excelente fertilidad femenina, tubérculos redondo-ovalados y está bien adaptado a la zona este de Canadá. La madurez del follaje es ligeramente más tardía que la de Kennebec. Asimismo, su rendimiento comercial más bajo es 78% superior al de Kennebec. Los valores de su gravedad específica, cocción, horneado y fritura en hojuelas son un poco más bajos que Kennebec. El clon F87084 es resistente al tizón tardío, *Verticillium dahliae,* tizón temprano y a los patotipos de verruga encontrados en Newfoundland. F87084 posee resistencia extrema a PVY y PVX. También es resistente al patotipo Ro 1 del nematodo del quiste de la papa. El análisis de la progenie indica que el clon F87084 posee alelos en condición duplex para los genes que controlan la resistencia extrema a PVX así como la resistencia al nematodo del quiste de la papa (Ro1).

INTRODUCTION

The mounting concerns about the quality of the environment, combined with the relatively heavy load of pesticides which is applied to the potato crop, places an increasing demand on the control of potato pathogens by genetic means. Although genetic sources of resistance to most potato pathogens are known to exist among various wild and cultivated potatoes, it still remains a formidable task to combine the various genes for resistance into single clones while at the same time avoiding the introduction of undesirable traits such as lack of adaptation,

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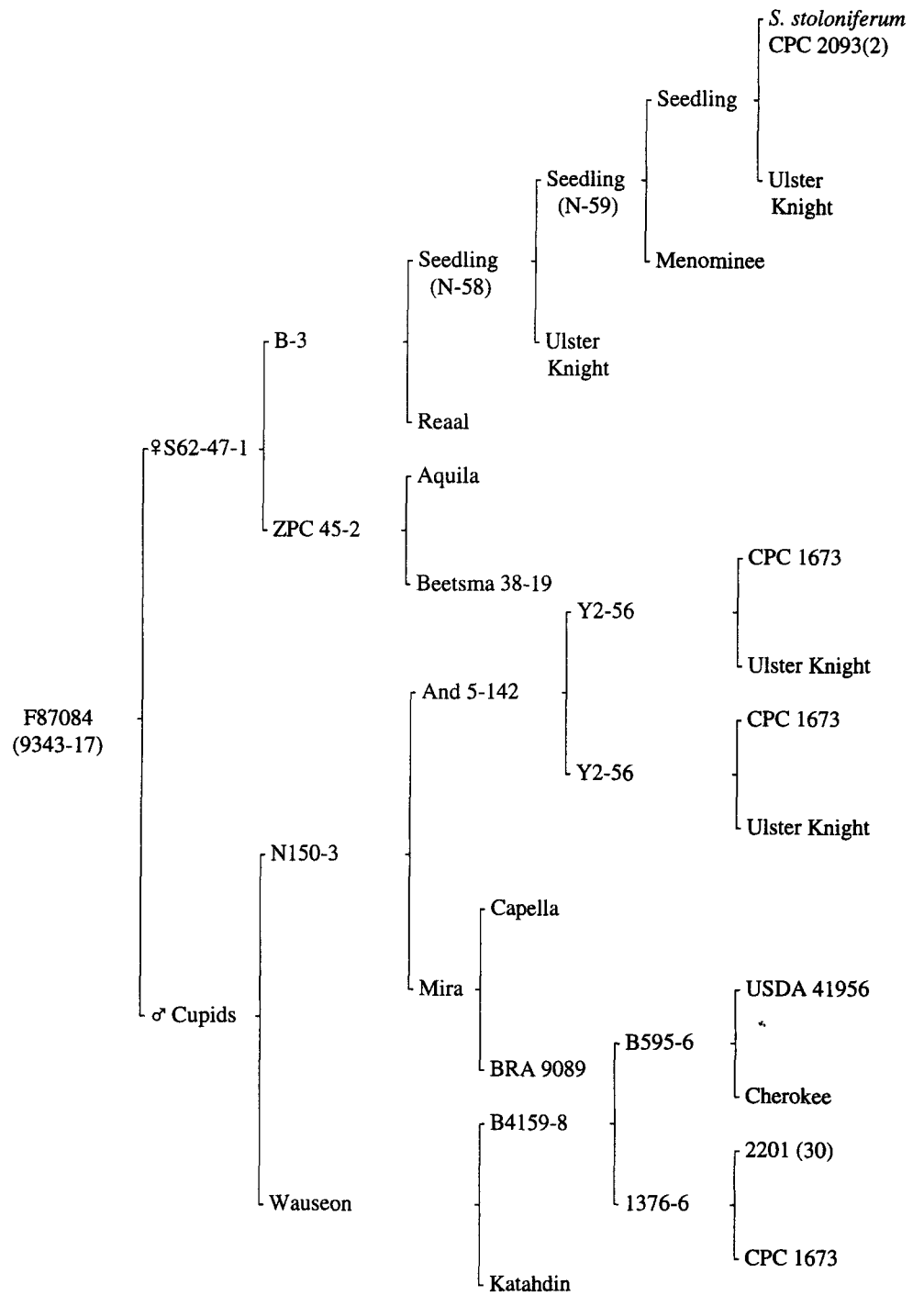
Abbreviations: CPC Commonwealth Potato Collection
EAPR European Association for Potato Research
PCN Potato Cyst Nematode
PLRV Potato Leafroll Virus
PVA Potato Virus A
PVX Potato Virus X
PVY Potato Virus Y, common strain
TGA Total Glycoalkaloids
aclSolanum acaule
dmsSolanum demissum
stoSolanum stoloniferum
tbrSolanum tuberosum

high levels of glycoalkaloids, or sexual sterilities. This report describes the accumulation of genetic resistances to several potato pathogens in an adapted, fertile clone.

PEDIGREE OF F87084

F87084, initially tested under seedling number 9343-17, is derived from a cross made by K. G. Proudfoot (KGP) between S62-47-1 (female) and Cupids (male). S62-47-1 is derived from a selection of the Commonwealth Potato Collection of *S. stoloniferum* (*sto*) CPC 2093 (2). The original *sto* introduction was backcrossed several times to *S. tuberosum* (*tbr*). This backcrossing program was conducted at the John Innes Institute in the U.K. during the late 1950s and early 1960s. S62-47-1 was selected by KGP at the Northern Ireland Department of Agriculture Plant Breeding Station for its desirable crop characteristics and resistance to late blight. The *tbr* backcross parents used include cultivars from the USA (Menominee), Northern Ireland (Ulster Knight), and the Netherlands (Reaal). In addition, the Dutch breeding clone ZPC 45-2, which was resistant to late blight (based on the R1 gene) as well as PLRV and PVY (Hogen Esch and Zingstra 1962) was also used in the development of S62-47-1. Cupids is a cultivar that was developed by KGP at the AAFC Atlantic Cool Climate Crop Research Centre in St. John's and released in 1986. This cultivar, which is resistant to the wart (*Synchytrium endobioticum*) pathotypes occurring in Newfoundland, the potato cyst nematode (pathotype Ro1), and is extremely resistant to PVX, currently has a full permanent registration in Canada. Cupids is briefly described by Barclay and Scott (1997). F87084 was selected at Fredericton from a sample of botanical seed provided by KGP to H. De Jong (HDJ) in 1984. The pedigree of F87084 is as follows:



MATERIALS AND METHODS

Pollen Germination and Vigor

Pollen germination and vigor were determined by placing three drops of a germination medium (20% α lactose, 50 ppm boric acid, 100 ppm calcium nitrate, 50 ppm magnesium sulfate, and 50 ppm potassium nitrate) in a concavity of a special microscope slide. Pollen was sprinkled on the medium after which the slide was placed in a covered petri dish lined with wet filter paper. The slides were incubated for 5 h at room temperature. Pollen germination was determined under a light microscope at 40 x magnification. Eight slides x three fields per slide were analyzed for both F87084 and Katahdin (control). Pollen tube vigor was scored on a scale of 1 (very weak) to 5 (very vigorous).

Screening Procedures for Disease Resistances

Fungi

A. Late blight, *Phytophthora infestans.*

Field screening tests were carried out by Dr. H.W. Platt at the AAFC Crops and Livestock Research Centre in Charlottetown, PE, during 1990, 1991, 1994 and 1995. At the time field tests were conducted, isolates used for inoculation were not routinely identified as to genotype or strain. In 1990, 1991, and 1994 the mating type was not specified but was most likely A1. In 1995, both A1 and a metalaxyl insensitive A2 mating type were detected in samples taken from the late blight screening plot. For a description of the test methods see Platt (1993, 1996, 1997).

B. Verticillium wilt, *Verticillium dahliae.*

Field screening was conducted with naturally occurring inoculum under typical field conditions in southern Idaho by Dr. D. Corsini, USDA/ARS/University of Idaho at Aberdeen. For a description of the test method see Corsini and Pavek (1993, 1994).

C. Early blight, *Alternaria solani.*

Field screening was conducted with naturally occurring inoculum under typical field conditions in southern Idaho by Dr. D. Corsini, USDA/ARS/University of Idaho at Aberdeen. For a description of the test method see Corsini and Pavek (1993,1994).

D. Fusarium dry rot, *Fusarium sambucinum* f.6.

Selections for dry rot evaluation were grown at Benton Ridge under similar management practices. Following harvest, the tubers were graded according to size and transported to the Potato Research Centre, Fredericton. Completely randomized samples consisting of three replicates of nine tubers each were placed in net bags, surface sterilized in 10% Javex, and rinsed with clean water. Each tuber was inoculated at two points midway between the stem and the bud end with 0.1ml of a 50,000-spore/ml solution of *Fusarium sambucinum* f.6 using a modified syringe as described by Boyd (1952). The blunt syringe tip punctures the flesh to a uniform depth and width of 5mm and simultaneously delivers a drop of inoculum. The tubers were incubated for 6 wk at 12 C at which point they were cut through the inoculation points and the extent of rot was estimated on a 1-9 scale of increasing susceptibility.

E. Wart, *Synchytrium endobioticum.*

F87084 was planted in six seasons from 1987-1994 in field plots at Avondale, NF, heavily infested with wart. Susceptible control cultivars were planted to determine if conditions were conducive to wart development. In Canada, wart disease occurs only in NF, usually in small home garden plots that have been in use for many years.

Bacteria

A. Common scab, *Streptomyces scabies.*

F87084 was tested for reaction to scab in a field plot heavily infested with *Streptomyces scabies* at the AAFC Potato Research Centre, Fredericton. Conditions favorable for the development of scab were maintained with high pH (6.8-7.0) and with applications of fresh manure. At harvest, tubers were rated for pustule type (1-5) and the extent of surface area with symptoms. Raw data were converted to a relative percentage of the nearest susceptible check. The percentage values were then indexed on a 1-9 scale of increasing susceptibility. Green Mountain usually has a value of 8 and Hindenburg 2 or 3 on this scale. In addition, field tests for resistance to common scab were conducted by Dr. D. Corsini, USDA/ARS/University of Idaho at Aberdeen, ID (Corsini and Pavek, 1993, 1994).

Viruses

A. PVX, PVY^O and PVA.

Plants of F87084 were dusted with carborundum and mechanically inoculated with sap extracts of either PVX, PVY^O or PVA that had been produced in tobacco cv. Sansum at the AAFC Potato Research Centre, Fredericton. At 3 to 4 wk post inoculation, the plants were tested by ELISA to detect infection by either PVX , PVY^O, or PVA. As the results of mechanical inoculation were negative for all three viruses, approach grafts to virus-infected tomatoes were performed. ELISA testing was used to confirm the presence or absence of virus in the scions of F87084 and the check cultivars.

B. Progeny tests for resistance to PVX and PVY^O.

Progenies were screened for extreme resistance to PVX and PVY^O in separate tests at the AAFC Potato Research Centre, Fredericton, as follows: scooped out eyes or small tubers were planted in the greenhouse in individual cells of planting trays along with appropriate control cultivars. Inoculum was produced in tobacco cv. Sansum. Just prior to inoculation the infected tobacco leaves were macerated in distilled water in a blender; the sap was strained through cheesecloth and mixed with carborundum (leaves : water : carborundum = 1: 50: 0.25). Progeny were inoculated at 6 wk post planting using an artist's air brush one or two times. Plants with typical symptoms of either PVX or PVY^O were removed and the surviving plants were tested with ELISA to confirm the presence or absence of infection.

Potato cyst nematode

A. Golden nematode, *Globodera rostochiensis*, Ro1.

F87084 was tested three times by Dr. B. B. Brodie, Cornell University, in a root ball test that is routinely used to test NY potato breeding selections. Juvenile nematodes are added to the potting mix and about 6 wk later the root mass is examined for the presence of cysts. Plants which support the development of less than five cysts per root ball are considered to be resistant. Progeny tests were conducted in the same manner using just one tuber per clone.

RESULTS AND CHARACTERISTICS OF F87084

Fertility

F87084 flowers well and has very good female fertility. The fruit set is good with a mean number of seeds per fruit ≥125. The pollen germination of F87084 was 21% as compared to 35% for Katahdin; the pollen tube vigour scores were 3 and 5 for F87084 and Katahdin, respectively. The fruit and seed set of F87084, when used as a male parent, is low. Under field conditions this selection produces a moderate amount of open-pollinated fruits.

Horticultural Features

A comparison of various horticultural traits for F87084 and Kennebec is presented in Table 1. The vine maturity of F87084 is slightly later than Kennebec. The tubers are round-oval, of medium size with high set and have heavily flaked, white skin (Fig. 1). The flesh color is white. During the seven-year period of 1990-1996 the marketable yield in terms of percentage of Kennebec has ranged from 49% to 118% with a seven-year mean of 78% of Kennebec. The mean specific gravity of F87084 was 1.072 as compared with 1.085 for Kennebec. The boil, bake, and chip scores of F87084 have also been somewhat lower than those for Kennebec.

Disease Resistances

In the three years (1990, 1991 and 1994) where mating type A1 occurred, the highest category of foliar disease for F87084 was 3 on a 1-9 scale of increasing susceptibility (Table 2). Unusually dry conditions in 1994 limited disease spread, and the scores for the three cultivars listed may be uncharacteristically low. Foliar infection in 1995 at 54% was higher than previously observed. This may reflect a more susceptible reaction of F87084 to the A2 mating type or a change in the incidence of pathogenic races in the inoculum. Tuber reaction to late blight differed according to mating type. F87084 appears to be more suscepible to

FIGURE 1.
Tuber type of F87084.

TABLE 1—*Means of horticultural traits of F87084 and Kennebec from 1990-1996.*

Trait	F87084	Kennebec
Vine maturity[1]	3.8	3.5
Marketable yield (T/ha)[2]	16.1	20.6
Specific gravity[3]	1.072	1.085
Boil score[4]	59	68
Bake score[5]	56	65
Chip[6] score 6.7C[7]	39	47
Chip[6] score reconditioned from 6.7C[8]	55	57
Dormancy[9]	7	6

[1]Vine maturity, measured on scale of 1 (early) to 5 (late). On this scale Norchip = 3.0, Kennebec = 3.5 and Russet Burbank = 4.0.
[2]Marketable yield - Canada No. 1 (for round tubers): 57.2-88.9 mm (2-1/4-3-1/2") + large: 88.9- 114.3 mm (3-1/2-4-1/2").
[3]Specific gravity: determined by the weight-in-air, weight-in-water method.
[4]Boil score: 50-60 = fair; 60-70 = good, relatively moist texture; >70 = good, relatively dry texture.
[5]Bake score: 55-65 = fair; 65-75 = good, relatively moist texture; >75 = good, relatively dry texture.
[6]Chip score based on AAFC colour charts: <50 = poor; 50-70 = moderate; 70-80 = good; >80 = excellent.
[7]Evaluated in January from 6.7 C.
[8]Stored at 6.7 C until January, then reconditioned for two weeks at 21 C.
[9]Dormancy, measured on a scale of 1 (very short) to 9 (very long).

the A2 mating type in these tests. In Idaho tests it has been resistant to early blight, *Alternaria solani* and verticillium wilt caused by *Verticillium dahliae* (Table 3). It is susceptible to dry rot caused by *Fusarium sambucinum* f.6. (Table 4). F87084 was tested in wart-infested plots at Avondale, NF, six times and was found to be resistant to the pathotypes occurring in NF. It was found to be very susceptible to common scab in field evaluations in both Fredericton, NB, and Aberdeen, ID (Tables 3 and 4). F87084 has extreme resistance to PVX , PVY^O, and PVA (Table 5). Some genotypes carrying the Ry_{sto} gene also react with extreme resistance to PVA, a virus closely related to PVY. This is also the case with F87084. F87084 was tested three times by Dr. B. B. Brodie and was found resistant to the potato cyst nematode (*Globodera rostochiensis*), pathotype Ro1. A progeny analysis for extreme resistance to PVX and resistance to the potato cyst nematode (PCN) indicated that F87084 is duplex for the genes for both of these traits (Table 6). A progeny analysis for extreme resistance to PVY^O (Table 7) indicates that F87084 is probably simplex for this gene.

Glycoalkaloid Content

The total glycoalkaloid (TGA) content from a sample of the 1995 crop indicated a value of 5.9 mg/100 g fresh weight (FW) as compared with 8.7 for Kennebec. The TGA content from a sample of the 1996 crop was 4.2 mg/100 g FW.

TABLE 2—*Comparative resistance of F87084 and several control cultivars to late blight at Charlottetown, PE.*

Late blight (foliage) Cultivar	1990[1]	1991[1]	1994[1]	1995[2]
F87084	3	2	0	54%
Green Mountain	8	8	0	92%
Dorita	2	2	0	56%
	Late blight tuber rot[3] (%)			
	1995 A1	1995 A2	1999 A2	
F87084	0	46	40	
Green Mountain	80	75	100	
Dorita	0	4	nt[4]	

[1]Percentage of foliage exhibiting symptoms to late blight. Data were analyzed by principal component analysis, Scott-Knott cluster analysis and indexed on a 0-9 scale (0 = immune, 9 = highly susceptible).
[2]Percentage of foliage exhibiting late blight symptoms.
[3]Occurrence of tubers exhibiting tuber rot following inoculation and storage for 24 days.
[4]Not tested.

DISCUSSION

As can be seen from its pedigree, F87084 can be traced back to very diverse germplasm sources. The late blight resistance of F87084 may have been partially derived from the Dutch cultivar Reaal. This cultivar is in *dms* cytoplasm and carries the R1 and R3 genes for late blight resistance (Hogen Esch and Zingstra 1962). Another potential source of late blight resistance

TABLE 3—*Comparative resistance of F87084 and several control cultivars to verticillium wilt, early blight and common scab at Aberdeen, ID.*

	Verticillium wilt[1]			Early Blight[1]			Common scab[2]		
Cultivar	1992	1993	1999	1992	1993	1999	1992	1993	1999
F87084	1	1.3	1.2	2.1	2.5	2.5	4	TR	4
Russet Burbank	5	8	5.7	5.2	7.5	7.3	0	TR	1.7
Russet Norkotah	9	nt[3]	8.7	8.4	nt	8.7	TR	nt	0.7
Shepody	5.4	5.3	5.8	5.7	5.8	7.7	1.6	1	3

[1]Scored on scale of 0 (none) to 9 (90-100% dead).
[2]Scored on scale of 0 (no scab) to 5 (100% culls due to scab).
[3]nt Not tested

TABLE 4—*Comparative resistance of F87084 and several cultivars to common scab and fusarium dry rot at Fredericton, NB.*

	Common scab		Fusarium dry rot			
Cultivar	1988[1]	1990[1]	1991[2]	1992[2]	1994[2]	1995[2]
F87084	7	9	7	4	4	4
Green Mountain	9	6	7	8	6	4
Hindenburg	3	3	nt[3]	nt	nt	nt
Shepody	nt	nt	3	3	3	3

[1]Scab score: tubers are rated for the extent and surface area affected relative to the susceptible check cultivar, Green Mountain, which is planted nearby. The values are indexed on a 1-9 scale of increasing susceptibility.
[2]Fusarium Dry Rot: the extent of dry rot is estimated from 1-9, using the diagram in the EAPR Disease Assessment Keys (Langerfeld 1987). The scale is reversed meaning that 9 indicates a highly susceptible reaction.
[3]nt Not tested

TABLE 5—*Comparative resistance of F87084 and several control cultivars to PVX, PVY and PVA at Fredericton, NB.*

	PVX	
	Mechanical inoculation	Grafting[1]
Cultivar	1997	1998
F87084	Negative	Negative
Green Mountain	Positive	Positive
Sebago	Positive	nt[4]
Saco	Negative	nt
Kennebec	nt	Positive

	PVY[o]			
	Mechanical inoculation			Grafting[2]
	1985	1986	1991	1997
F87084	Negative	Negative	Negative	Negative
Shepody	Positive	Positive	nt	nt
Serrana Inta	Negative	Negative	nt	nt
Agitato	Negative	nt	nt	nt
Norchip	nt	Positive	nt	nt
F79070	nt	Negative	Negative	Negative
Saco	nt	Positive	nt	nt
Kennebec	nt	Negative	Negative	nt
Green Mountain	nt	nt	Positive	nt
Russet Burbank	nt	nt	Positive	Positive

	PVA	
	Mechanical inoculation	Grafting[3]
F87084	Negative	Negative
Green Mountain	Positive	nt
Shepody	Negative	Negative
Yukon Gold	Negative	nt
Russette	Negative	Negative
Kennebec	nt	Positive
Russet Burbank	nt	Positive

[1]Grafting to PVX positive tomato cv. Rutgers.
[2]Grafting with PVY positive Potato cv. Russet Burbank scions.
[3]Grafting to PVA positive tomato cv. Rutgers.
[4]nt Not tested

is ZPC 45-2. This clone has the R1 gene (Hogen Esch and Zingstra 1962), which may have derived from Aquila (Müller, 1951). In addition, *sto* CPC 2093 may also have contributed to the late blight resistance of F87084.

The wart resistance of F87084 can, via Cupids, N150-3, Y2-56, and And 5-142, be traced back to CPC 1673. The German cultivar Mira (syn. Ora) has also been a major contributor of wart resistance in F87084. Mira represents an assembly of genes conferring resistance to several Western European pathotypes of wart (Maris 1961). The male parent of Mira, BRA 9089, derived its wart resistance from ancestors that include a Chilean cultivar, the Polish cultivar Switez, and a local cultivar from the German region of Frankonia (Ross 1986).

Although at least two ancestors of F87084 have a moderate to good resistance to common scab (Wauseon [Cunningham *et al.* 1968] and Menominee [Wheeler *et al.* 1944]), this resistance was not transmitted to F87084. The female parent, S62-47-1, was also susceptible to common scab in plots in Newfoundland.

The progenies between F87084 and AC Chaleur and Cherokee respectively fit a 5:1 segregation ratio for extreme resistance to PVX (Table 6). Since AC Chaleur and Cherokee are both susceptible to PVX, it appears that F87084 is duplex for extreme resistance to PVX. The progeny from A11208-01 x F87084 closely fits a 35:1 segregation ratio. Such a ratio is expected when both parents are duplex for the trait in question. Therefore it appears that both A11208-01 and F87084 are duplex for the gene conferring extreme resistance to PVX. The family derived from F87084 x AC Chaleur does not have a very close fit for a 5:1 segregation ratio for both extreme resistance to PVX and resistance to the PCN. As discussed elsewhere in this paper, segregation distortion for gene(s) conferring extreme resistance to PVX is not uncommon (Ritter *et al.* 1991). Nevertheless, the balance of the evidence appears to indicate that F87084 is duplex for this trait. At least one of the alleles for the extreme resistance to PVX of F87084 can, via Cupids, be traced back to And 5-142 and may in turn have been derived from CPC 1673. It appears that F87084 is also duplex for the gene controlling PCN resistance (Table 6). At least one of the alleles for resistance to the PCN can, via Cupids and Wauseon, be traced back to CPC 1673. This is likely the *H1* locus (Gebhardt 1994). It is of interest to note that of the two known genes that each confer extreme resistance to PVX (*Rx1* and *Rx2*), one (*Rx2*) is linked to the *H1* locus (Gebhardt 1994). The data used in this study were collected from different

TABLE 6—*Segregation for extreme resistance to PVX and resistance to potato cyst nematode (PCN) in progenies of F87084.*

Progenies		PVX						PCN					
		Observed		Expected (5:1)				Observed		Expected (5:1)			
Female	Male	R	S	R	S	Chi Sq.	P	R	S	R	S	Chi Sq.	P
F87084	AC Chaleur	75	25	83.3	16.7	4.9	.02-.05	14	7	17.5	3.5	4.2	.02-.05
F87084	Cherokee	81	18	82.5	16.5	0.2	.50-.75	13	1	11.7	2.3	0.9	.25-.50
Total		156	43	165.8	33.2	3.5	.25-.50						
				Expected (35:1)									
A11208-01	F87084	98	2	97.2	2.8	0.2	.50-.75	23	5	23.3	4.7	0.02	.75-.90
Total								50	13	52.5	10.5	0.71	.25-.50

samples of the same progenies; it is therefore not possible to determine whether or not there is linkage in F87084 between the genes conferring extreme resistance to PVX and PCN resistance. The purpose of this study is not inheritance of specific traits, but rather the description of a potentially very valuable parent. The duplex condition for extreme resistance to PVX and resistance to the PCN in F87084 facilitates the transmission of these resistances to its progeny; when crossed with susceptible parents, a high proportion of the progeny is resistant.

The segregation for PVY^O resistance in six progenies of F87084 is presented in Table 7. For some of these progenies the segregation closely fits a 3 : 1 ratio. This is a ratio that can be expected for a segregation from a simplex x simplex cross. Such progenies could possibly also result from an inadvertent self pollination of the female parent. The segregation of some progenies also fit a 5:1 ratio. Such a ratio can be expected from a duplex x nulliplex cross. However, in the progenies derived from crossing F87084 with Russette and B5141-6, the segregation closely fits a 1:1 ratio. This is a ratio that can be expected from a simplex x nulliplex cross. There is no clear explanation for the apparent discrepancy between these progenies. A possible reason for this anomaly may be a distorted segregation. Distorted segregation ratios for extreme resistance to PVY have been observed in other progenies which have been generated at the AAFC potato breeding program in Fredericton (data not shown) and others (Dolnicar 1995; Flis 1995). There are several hypotheses that may be able to explain this phenomenon:

(a) Hybrids between (tetrasomic) *tbr* and disomic tetraploids such as *S. acaule (acl)* and *sto* are known to have irregular chromosome pairing (Hermsen 1994; Matsubayashi 1991). If specific genes, which have been derived from such disomic tetraploids, are located in chromosome regions that do not pair well with *tbr* chromosomes then distorted segregation may occur. For example, Ritter *et al.* (1991) found a distorted segregation for the *Rx2* gene. This gene is located on chromosome 5, in a region where reduced recombination and segregation distortion for other genes have also been observed. Although in that study the origin of *Rx2* could not be traced back with absolute certainty, there is a strong possibility that it originated with *acl* (Ritter *et al.* 1991). In general, in recent mapping experiments aberrant segregation ratios have been found in several regions of the potato genome (Gebhardt, pers. comm.). The PVY^O resistance of F87084 can (at least in part) be traced back to *sto* CPC2093. The inheritance of PVY resistance in CPC2093 has been described

TABLE 7—*Segregation for extreme resistance to PVY in progenies of F87084.*

Progenies		Observed		Expected								
				1:1			3:1			5:1		
Female	Male	R	S	R	S	Chi Sq	R	S	Chi Sq	R	S	Chi Sq
F87084	Wischip	74	26	50	50	23	75	25	0.1	83.3	16.7	5.3
F87084	AF186-2	77	23	50	50	29.2	75	25	0.2	83.3	16.7	2.8
F87084	CS7232-4	82	18	50	50	41	75	25	2.6	83.3	16.7	0.1
F87084	F58050	68	32	50	50	13	75	25	2.6	83.3	16.7	16.8
F87084	Russette	47	51	49	49	0.2	73.5	24.5	38.2	81.7	16.3	88.6
F87084	B5141-6 (Lenape)	52	47	49.5	49.5	0.3	74.2	24.8	26.5	82.5	16.5	67.7

by Cockerham (1970) as controlled by a single dominant gene (Ry_{sto}). It is conceivable that this gene is located on a chromosome region with reduced recombination and that this, in turn, contributes to the distorted segregation ratios.

(b) In a study on the inheritance of extreme resistance to PVY, Flis (1995) observed a surplus of susceptible genotypes in several progenies. Hypotheses proposed by Flis (1995) include inheritance schemes that involve more than one single dominant gene as well as modifications of resistance depending on virus isolate and conditions of virus detection.

(c) Some of the male parents may have contributed a certain level of PVY resistance to their respective progenies. For example, this may have been the case with the progenies between F87084 and Wischip, AF186-2, CS7232-4, and F58050.

The results presented here are not intended as an inheritance study but further investigations into the inheritance of extreme resistance to PVY are clearly needed. The release of this selection represents an example of the building and assembling of many desirable traits, including disease resistances, that is possible with "traditional" breeding methods.

AVAILABILITY

F87084 is available as *in vitro* plantlets from the AAFC Potato Research Centre, PO Box 20280, Fredericton, NB, E3B 4Z7. EM: murphya@em.agr.ca.

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LITERATURE CITED

Barclay, G.M. and P. Scott (eds.) 1997. Potato Varieties in Canada. New Brunswick Department of Agriculture and Rural Development, Florenceville, NB, p. 44.

Boyd, A.E.W. 1952. Dry rot resistance of potato. IV. Laboratory methods used in assessing variation in tuber susceptibility. Ann Rev Appl Biol 39:322-329.

Cockerham, G. 1970. Genetical studies on resistance to potato viruses X and Y. Heredity 25:309-348.

Corsini, D.L. and J.J. Pavek. 1993. Evaluation of potato breeding selections and cultivars for resistance to field diseases, 1992. *In:* D.S. Wysong (ed), Biological and Cultural Tests for Control of Plant Diseases. v.8. APS Press, St. Paul, MN. p. 52.

Corsini, D.L. and J.J. Pavek. 1994. Evaluation of potato breeding selections and cultivars for resistance to field diseases, 1993. *In:* D.S. Wysong (ed), Biological and Cultural Tests for control of Plant diseases. v. 9. APS Press, St. Paul, MN. p. 74.

Cunningham, C.E., R.V. Akeley, L.C. Peterson, and T.E. Snyder. 1968. Wauseon: A new potato variety resistant to golden nematode with good processing quality. Am Potato J 45:146-149.

Dolnicar, P. 1995. The segregation for extreme resistance in progeny infected with different isolates of PVYn strain. Potato Res 38:434 (Abstr).

Flis, B. 1995. Inheritance of extreme resistance to potato virus Y in potato. Potato Res 38 :199-210.

Gebhardt, C. 1994. RFLP mapping in potato of qualitative and quantitative genetic loci conferring resistance to potato pathogens. Am Potato J 71:339-345.

Hermsen, J.G.Th. 1994. Introgression of genes from wild species, including molecular and cellular approaches. *In:* J.E. Bradshaw and G.R. Mackay (eds), Potato Genetics. CAB International. pp. 515-538.

Hogen Esch, J.A. and H. Zingstra. 1962. Geniteurslijst voor aardappelrassen 1962. C.O.A. Wageningen.

Langerfeld, E. 1987. Methoden bei der Prüfung der Reaktion von Kartoffelsorten gegen Lagerfäuleerreger der Gattung Fusarium. *In:* Potato Disease Assessment Keys. Eur Assoc Potato Res, Committee for disease assessment. pp. 101-110.

Maris, B. 1961. Races of the potato wart causing fungus *Synchytrium endobioticum* (Schilb.) Perc. and some data on the inheritance of resistance to race 6. Euphytica 10:269-276.

Matsubayashi, M. 1991. Phylogenetic relationships in the potato and its related species. *In:* T. Tsuchiya and P.K. Gupta (eds), Chromosome Engineering in Plants: Genetics, Breeding, Evolution. Developments in Plant Genetics and Breeding, 2B. Elsevier. pp. 93-118.

Müller, K.O. 1951. Über die Herkunft der W-Sorten, ihre Entwicklungsgeschichte und ihre bisherige Nutzung in der praktischen Kartoffelzüchtung. Z Pflanzenz 29:36-387.

Platt, H.W. 1993. Response of potato breeding program early screening selections and cultivars to late blight, 1991. *In:* D.S. Wysong (ed), Biological and Cultural Tests for Control of Plant Diseases. v. 8. APS Press, St. Paul, MN. p. 44.

Platt, H.W. 1996. Response of potato breeding program early generation selections and cultivars to foliar late blight, 1994. *In:* C.H. Canaday (ed), Biological and Cultural Tests for Control of Plant Diseases. v. 11. APS Press, St. Paul, MN. pp. 66.

Platt, H.W. 1997. Late blight tuber rot response of potato breeding lines and cultivars to A1 and A2 mating types of the pathogen, 1995. *In:* C.H. Canaday (ed), Biological and Cultural Tests for Control of Plant Diseases. v.12. APS Press, St. Paul, MN. pp. 91.

Ritter, E., T. Debener, A. Barone, F. Salamini, and C. Gebhardt. 1991 RFLP mapping on potato chromosomes of two genes controlling extreme resistance to potato virus X (PVX). Mol Gen Genet 227:81-85.

Ross, H. 1986. Potato Breeding–Problems and Perspectives. Parey. 132 p.

Wheeler, E.J., F.J. Stevenson, and H.C. Moore. 1944. The Menominee potato: A new variety resistant to common scab and late blight. Am Potato J 21:305-311.