Founding Clones, Major Contributing Ancestors, and Exotic Progenitors of Prominent North American Potato Cultivars

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ABSTRACT

Neither founding clones nor major genetic contributors to modern North American potato cultivars have been systematically identified. Available pedigrees, through 12 generations, were used to identify founding clones and major contributing ancestors (MCAs), to outline relationships among these clones, to determine the genetic contribution of MCAs and exotic germplasm to prominent cultivars, and to draw conclusions about the gene base of prominent North American cultivars. Based on 1996 certified seed acreage, 46 cultivars were identified as prominent, of which 44 had published pedigrees. Using this pedigree data, 12 MCAs consisting of four types were identified: land race types including Daber and Sutton's Flourball; immediate descendants of land race types including Busola, Early Rose, Garnet Chili, Imperator, Richter's Jubel, and Triumph; early USDA releases including Chippewa, Earlaine, and Katahdin; and one derivative of a German *Solanum demissum* x *S. tuberosum* population designated Germ. No. 3895-13. These clones appeared in the pedigrees of from 61 to 100% of the 44 most prominent North American cultivars. Some MCAs appeared numerous times in the pedigrees of the cultivars with the maximum being Busola, which appeared in the pedigree of NorDonna 94 times. Across the 44 cultivars, the genetic contribution of MCAs averaged from 1.4% for Daber to 23.2% for Katahdin. A positive genetic contribution by exotic germplasm was present in 34 of the 44 cultivars. Krantz, Russet Nugget, Conestoga, and Yukon Gold had exotic germplasm contributions of 49.5, 34.1, 32.3, and 31.3%, respectively.

Accepted for publication February 20, 1999.
ADDITIONAL KEY WORDS: *Solanum tuberosum* L., pedigrees, genetic contribution, exotic germplasm, gene base.
Paper No. 98719 in the Idaho Agricultural Experiment Station Series.

INTRODUCTION

Over 84 potato cultivars were grown for certified seed in North America as of 1996 (National Potato Council, 1997). Dates for introduction of these cultivars range from 1876 up until just a few years ago (Chase, 1984, with updates). In spite of the disparity of age among these cultivars, current thinking is that they share extensive common ancestry (Mendoza and Haynes, 1974; Plaisted and Hoopes, 1989). The resulting narrow gene base among commercially grown potatoes gives concern for the stability of production. A narrow gene base results in homogeneity for resistance genes, leaving all or most of the crop susceptible to severe damage by pests or diseases. An example of such a disease situation is that presented by the new metalaxyl resistant races of late blight, to which North American potato cultivars are universally susceptible (Inglis *et al.*, 1996).

Hawkes (1979) discussed the genetic diversity of potato germplasm among European cultivars. Because North American potatoes were originally imported from Europe, and exchange of germplasm has occurred freely between Europe and North America, his comments are equally pertinent to North American cultivars. Hawkes listed four introduction events that formed the basis of modern potato germplasm. The first two were *Solanum tuberosum* subsp. *andigena* introductions from South America into Spain and England around 1570 and 1590, respectively. No other introductions

Abbreviations:
MCA = major contributing ancestor, acl = *Solanum acaule*, adg = *Solanum tuberosum* subsp. *andigena*, chc = *Solanum chacoense*, dem = *Solanum demissum*, ktz = *Solanum kurtzianum*, mag = *Solanum maglia*, phu = *Solanum phureja*, rap = *Solanum raphanifolium*, sim = *Solanum simplicifolium*, spg = *Solanum spegazzinii*, stn = *Solanum stenotomum*, tor = *Solanum toralapanum*.

were recorded until around 1830 when the South American cultivar Daber was imported into Germany. Finally, in 1861, Goodrich imported Rough Purple Chili into the US. Evidence suggests that until the 1920s, these four introductions formed the genetic foundation of all European and North American cultivars. The situation naturally led to a narrow gene base, made even narrower by germplasm losses during the European late blight epidemics of the 1840s.

With the introduction of *Solanum demissum* from Mexico into Europe in the early 1900s, and its subsequent use in breeding, a trend for incorporation of unrelated germplasm was established. This has continued for the past 70 years, and a high percentage of commercially prominent North American cultivars contain genes from "wild" species. However, the overall gene base of potatoes remains quite narrow. Evidence for continued common ancestry among North American cultivars was given by Mendoza and Haynes (1974), who established the presence of a high level of coancestry among cultivars introduced prior to 1969. No inbreeding or coancestry values have been provided for North American cultivars released since that time.

Pedigree information can be used to evaluate a crop gene base using any of a number of strategies. One such strategy is to find the founding varieties and major contributing ancestors (MCAs) and to determine the genetic contribution of these clones to prominent cultivars. No systematic effort has been made to identify the founding clones and MCAs of North American potato cultivars. The goals of this research were to use available pedigree information to identify the founding clones and MCAs for 44 prominent cultivars, outline relationships among these founding clones, calculate the genetic contribution of MCAs to prominent cultivars, and to determine the genetic contributions of exotic germplasm.

MATERIALS AND METHODS

For this study, commercially prominent cultivars were defined as those with minimum 1996 certified seed production of 200 acres in 1996. Using the 1997 National Potato Council's Potato Statistical Yearbook, it was determined that 46 cultivars met this criterion. Two of these cultivars, Irish Cobbler and White Rose, have uncertain parentage and were eliminated from the list. The remaining forty-four cultivars, their year of introduction, and parentage are listed in Table 1. These cultivars have a range of published introduction dates from 1914 through 1995 (Chase, 1984, with updates).

With the parents of each cultivar being defined as the first generation (one generation removed from the cultivar of interest) the known pedigree of each cultivar was extended 12 generations. Pedigree information was taken from published release descriptions, as listed in the Potato Variety Inventory (Chase, 1984), assorted cultivar handbooks (Clark and Lombard, 1951; Darling, 1959; Rathlef, 1932; Salaman, 1926; Stevenson and Clark, 1937; Stuart, 1915 and 1929; Swiezynki *et al.*, 1997), published papers (Akeley *et al.*, 1948; Folsom, 1945; Horsfall, 1972; Reeves *et al.*, 1980), National Potato Germplasm Reports (Published since 1943 by the USDA, Beltsville), and from the records of numerous breeders.

Using the pedigree information, lists of both founding clones and major contributing ancestors were compiled for the 44 cultivars. Founding clones were those of unknown ancestry (pedigree dead-ends) originating prior to the advent of public breeding programs in the early 1900s.

Major contributing ancestors (MCAs) were those which met two criteria: 1) those found in the ancestries of the majority of the 44 prominent cultivars; and 2) those which contributed through multiple first-generation progeny. This last criterion was intended to help identify clones breeders used successfully as parents and to eliminate clones which served simply as genetic conduits to or from the major contributors.

For each MCA, the percentage of descendants among the prominent cultivars was calculated. In addition, the number of times ancestors appeared in the pedigree was counted and the genetic contribution to each cultivar computed using the method employed by Lansari *et al.* (1994). The calculation of genetic contribution was based on the assumption that the process of selection does not change the random contribution of alleles from ancestors. Relationships among MCAs were mapped. The genetic contribution of exotic germplasm (wild species or clones with no known relationship with the founding clones or MCAs) was determined for each prominent cultivar. Finally, the information generated was used to reach conclusions about the gene base of modern North American potato cultivars.

RESULTS AND DISCUSSION

For most prominent cultivars, only limited pedigree information was available (Table 1). Within seven to ten generations, the majority of pedigree branches terminated at open pollinated progenitors or those with unknown parentage. Through twelve generations, there are 8,190 possible ancestors. Information about only a fraction of this number

TABLE 1.—*Prominent North American potato cultivars grown on 200 or more seed acres in 1996.*

Cultivar	Parentage	Date of Introduction	Percentage of Possible Ancestry Available[1]
AC Novachip	F68061 x F66011	1991	8.2
Andover	Allegany x Atlantic	1995	5.5
Atlantic	Waseon x B5141-6 (Lenape)	1976	5.1
CalWhite	Pioneer x BC8370-4	1995	16.4
Cascade	B3820-14 x PI214372	1969	2.7
Centennial Russet	Nooksack x W12-3	1976	8.9
Century Russet	A6789-7 x A6680-5	1995	14.5
Chieftain	LA 1354 x IA 1027-18	1966	4.5
Chipeta	WNC612-13 x Wischip	1993	14.3
Conestoga	G7063 x G6652	1982	15.0
Frontier Russet	A66102-16 x WN330-1	1990	13.4
Goldrush	ND450-3Russ x Lemhi Russet	1992	25.2
Itasca	MN304.72-10 x ND58-3	1994	19.2
Kanona	Peconic x GN bulk	1988	1.4
Katahdin	USDA 40568 x USDA 24642	1932	0.3
Kennebec	B127 x USDA X96-56	1948	1.8
Krantz	MN366.65-3 x G6743-5	1985	6.1
LaChipper	Cayuga x Green Mountain	1962	7.9
LaRouge	LA02-5 (LaSoda x Progress) self	1962	4.3
Mainestay	AF431-9 x ? (open pollination)	1995	5.3
Monona	B1268-46 x B1299-15	1964	1.4
Nooksack	Kennebec x A501-13	1973	4.5
Norchip	ND4731-1 x M5009-2	1968	4.4
NorDonna	ND206-1R x ND821-6R	1995	29.2
Norland	RedKote x ND626	1957	5.6
NorValley	Norchip x ND860-2	1996	22.5
NorWis	RD289-18 x Monona	1990	3.4
Onaway	USDA X96-56 x Katahdin	1956	1.4
Ontario	Richter's Jubel x USDA 44537	1946	0.8
Pike	Allegany x Atlantic	1995	5.5
Ranger Russet	Butte x A6595-3	1991	13.3
Red LaSoda[2]	Triumph x Katahdin	1953	0.4
Red Pontiac[3]	Triumph x Katahdin	1945	0.4
Red Ruby	Bison x MN11.76-10	1994	9.3
Russet Burbank[4]	Early Rose x ?	1914	<0.1
Russet Norkotah	ND9526-4Russ x ND9687-5Russ	1987	17.5
Russet Nugget	Krantz x AND71609-1	1989	13.7
Sangre	Viking x A6356-9	1982	9.7
Sebago	Chippewa x Katahdin	1938	0.7
Shepody	Bake-King x F58050	1980	4.8
Snowden	B5141-6 (Lenape) x Wischip	1990	11.6
Superior	USDA X96-56 x MN59.44	1961	6.7
Viking	Nordak x Redskin	1963	5.4
Yukon Gold	W5279-4 x Norgleam	1980	3.5

[1]Indicates the amount of pedigree information expressed as the percentage known of the 8,190 possible ancestors through 12 generations. Repeat appearances by ancestors were counted separately.
[2]Red LaSoda is a clonal selection of LaSoda (introduced in 1948).
[3]Red Pontiac is a clonal selection of Pontiac (introduced in 1938).
[4]Russet Burbank is a clonal selection of Burbank (introduced in 1876).

was available for each of the prominent cultivars. The highest number accumulated (including all repeating appearances for all ancestors) was for NorDonna with 2391 (29.2%), while the lowest was for Russet Burbank with 3 (<0.1%). The average known ancestry for the 44 cultivars, as a percentage of the total possible, was 7.8% with most falling in the range of 0.9 to 15.0%.

The consequence of the dearth of pedigree information was that any estimates of genetic contribution were underestimated. However, computation of a minimum genetic contribution was possible and provided valuable information concerning the diversity of the gene base among prominent North American potato cultivars.

The pedigrees revealed a total of 20 founding clones for prominent North American cultivars (Table 2). These clones

TABLE 2.—*Founding clones of prominent North American potato cultivars, percentage of cultivars descended from each founder, and well-known and/or important descendants.*

Clones	Percent of Cultivars as Descendants	Well Known/ Important Descendants
North American Origin		
Aroostook Wonder	98	Chippewa, Katahdin
Carman No. 3	5	Beltsville USDA seedlings
Carter	52	Early Vermont, Excelsior, Keeper, Silverskin
Charles Downing	34	Houma
Early Sunrise		Hindenberg, Busola
Irish Cobbler	70	Earlaine, Minnesota seedlings
Kepplestone Kidney	14	Beltsville USDA seedlings
Lookout Mountain	20	Progress, Minnesota seedlings
Rural New Yorker No. 2	95	Chippewa, Katahdin
Western Red	50	White Peachblow, Populair, Minnesota seedlings
English Origin		
Seed	73	Reichskanzler, Petronius, Earlaine
Sutton's Flourball	98	Hermann, Busola, Chippewa, Katahdin
White Rocks	98	Paterson's Victoria, Imperator, Busola
German Origin		
Deutches Reich	2	Parnassia, Canadian seedlings
Fransen	11	Eigenheimer, Populair, Aberdeen USDA seedlings
Hamburger Eierkartoffel	5	Populair, Aberdeen USDA seedlings
Spate Dauer	73	Victoria Auguste, Richter's Jubel
Russian Origin		
Trophime	5	Populair, Aberdeen USDA seedlings
South American Origin		
Daber	98	Wilhelm Korn, Reichskanter, Busola, Earlaine
Rough Purple Chili	100	Garnet Chili, Early Rose, Busola, Earlaine

[1]Origin of the clones designated Early Sunrise and Kepplestone Kidney are not known with certainty.

were in the pedigrees of from 2 to 100% of the 44 cultivars. Ten of the founding clones were of North American, three of English, four of German, one of Russian, and two of South American origin. All founders were the clonal equivalent of land races or were the products of mid to late nineteenth century breeding efforts.

Following careful evaluation of the 44 pedigrees, and using the established criteria, twelve MCAs were identified for the 44 prominent cultivars. The clones, their parentage, and origins are found in Table 3. Two contributors, Garnet Chili and Early Rose, were found in the ancestry of all 44 prominent cultivars (Table 4). Five additional clones, Busola, Daber, Imperator, Katahdin, and Sutton's Flourball were in the ancestry of over 90% of the cultivars. The other five contributing clones were present in over 60% of the pedigrees. In many cases, a lack of an MCA in a cultivar's ancestry was due, in part, to that cultivar being older than the MCA.

The MCAs fell into one of four categories, 1) clonal equivalents of land race types, 2) immediate descendants of land race types that were used as parents in Europe and North America, 3) early USDA releases, and 4) progeny from the early 1900 German late blight resistance breeding program involving *Solanum demissum* Lindl. The land race types are those with unclear origins and ancestry, and include Daber and Sutton's Flourball. Daber is an old South American cultivar imported into Germany, while Sutton's Flourball is an old English cultivar with uncertain background. Immediate descendants of land race types included Busola, Early Rose, Garnet Chili, Imperator, Richter's Jubel, and Triumph. Early USDA releases identified as MCAs included Chippewa, Katahdin, and Earlaine.

The MCA identified as Germ. No. 3895-13 is an open pollinated seedling from a late blight resistant population developed in Germany using hybrids between *S. tuberosum* and *S. demissum*. It is placed in a class by itself because of its species background and the fact that its *Solanum tuberosum* L. background is unknown. However, given that it was developed in the same country where several other founding clones and MCAs originated, it is likely related to some of the other German clones.

The pedigrees revealed complex relationships among the founding clones and MCAs (Figure 1). This chart suggests rapid movement of germplasm among the early breeding programs of many countries. Early Rose influenced cultivar development in Germany and other parts of Europe and is in the ancestry of Imperator, Richter's Jubel, and Busola. Daber and Sutton's Flourball are in the ancestry of Busola, a Polish-Russian cultivar. Busola, Imperator, Richter's Jubel, and Sutton's Flourball were imported into the US by breeders around the time the USDA breeding program began. The

TABLE 3.—*Parentage and origin of major contributing ancestors of prominent North American potato cultivars.*

Major Contributin Ancestor	Parentage	Origin
Busola	Alabaster x Furstin Hatzfeld	Introduced prior to 1914. Brought into the U.S. from Russian Poland in 1914. (Folsom, 1945; Rathlef, 1932)
Chippewa	USDA 40568 x USDA 24642	Released in 1933 by the Beltsville USDA breeding program. (Darling, 1959)
Daber	Unknown	Imported into Germany from South America around 1830. Never introduced into North America. (Rathlef, 1932)
Earlaine	Irish Cobbler x USDA 43055	Released in 1938 by the Beltsville USDA breeding program. (Darling, 1959)
Early Rose	Garnet Chili x ?	Originated in 1861 by Albert Bresee of Vermont. (Darling, 1959)
Garnet Chili	Rough Purple Chili x ?	Originated in 1853 by C.E. Goodrich of New York. (Darling, 1959; Plaisted and Hoopes, 1989)
Germ. No. 3895-13	Open pollinated seedling of a German derived S. *demissum* population.	Developed from a population imported from K.O. Müller in Germany. Brought into the U.S. around 1908. (Plaisted and Hoopes, 1989; Akeley *et al.*, 1948; Stevenson and Clark, 1937)
Imperator	Early Rose x Paterson's Victoria	Originated in 1875 by William Richter of Germany. No documented introduction in North America. (Salaman, 1926)
Katahdin	USDA 40568 x USDA 24642	Released in 1935 by the Beltsville USDA breeding program. (Darling, 1959)
Richter's Jubel	Victoria Auguste x Richter's S78-92	Originated prior to 1900 by William Richter of Germany. Introduced to the U.S. prior to 1937 by USDA breeders. (Folsom, 1945; Plaisted and Hoopes, 1989)
Sutton's Flourball	Unknown	Originated prior to 1880 in the U.K. Imported into the US prior to 1923. (Stevenson and Clark, 1937)
Triumph	Peerless x Seedling of Early Rose	Originated in 1878 by B.K. Bliss and sons of Connecticut. (Darling, 1959)

TABLE 4.—*Percentage of 44 prominent North American potato cultivars descended from, and the documented first generation progeny for, each of 12 major contributing ancestors.*

Major Contributing Ancestor	Percent of Prominent cultivars As Descendants	First Generation Progeny With Ancestral Ties to Prominent cultivars
Busola	98	Petronius, USDA 40238, USDA 40568, USDA 48774
Chippewa	80	B127, B1299-15, B2067-52, B2068-23, Sebago, USDA 44537, W13-253
Daber	98	Odin, Pommerania, Prof. Wohltmann, Reichskanzler, Wilhelm Korn
Earlaine	70	A102-35, B24-58, B56-1, B56-11, Delta Gold, F43021, Teton, USDA 45075, USDA 46952, USDA X247-24, USDA X247-44, USDA X247-48, USDA X499-A, USDA X792-24, USDA X792-88, USDA X792-94, USDA X96-44, USDA X96-56, USDA X96-140
Early Rose	100	Burbank, Early Ohio, Imperator, Silverskin, unnamed seedling
Garnet Chili	100	Early Rose, Early Vermont, Peerless
Germ. No. 3895-13	61	USDA X44-12, USDA X96-44, USDA X96-56, USDA X96-140
Imperator	98	Helios, Imperia, Maercker, Neue Imperator, President, Victoria Auguste
Katahdin	93	1441-8, B127, B1268-46, B3511-17, B3820-14, Cayuga, F34011, F43026, F45019, Houma, LaSoda, MN66-5, MN80-7, MN9-4, Mohawk, ND9-4-1, NEB.101.40-3, Onaway, Peconic, Pontiac, RD3-22, Reddick 421, Saranac, Sebago, Sequoia, USDA 44537, USDA 45075, USDA X1241-91, USDA X1276-179, USDA X444-12, USDA X627-126, USDA X627-213, USDA X927-3, US-W1, W13-253, W5279-4, W5289-2, Wauseon
Richter's Jubel	73	Hindenburg, Imperia, Menominee, MN43, MN43.39-6-40, Ontario, Parnassia, USDA X245-52, USDA X245-186, USDA X499-A, USDA X528-170, USDA X528-229, USDA X528-349.
Sutton's Flourball	98	Hermann, Juno, USDA 24642
Triumph	77	F43021, LaSoda, ND217-5, NEB.101.40-3, Pontiac, USDA 40154

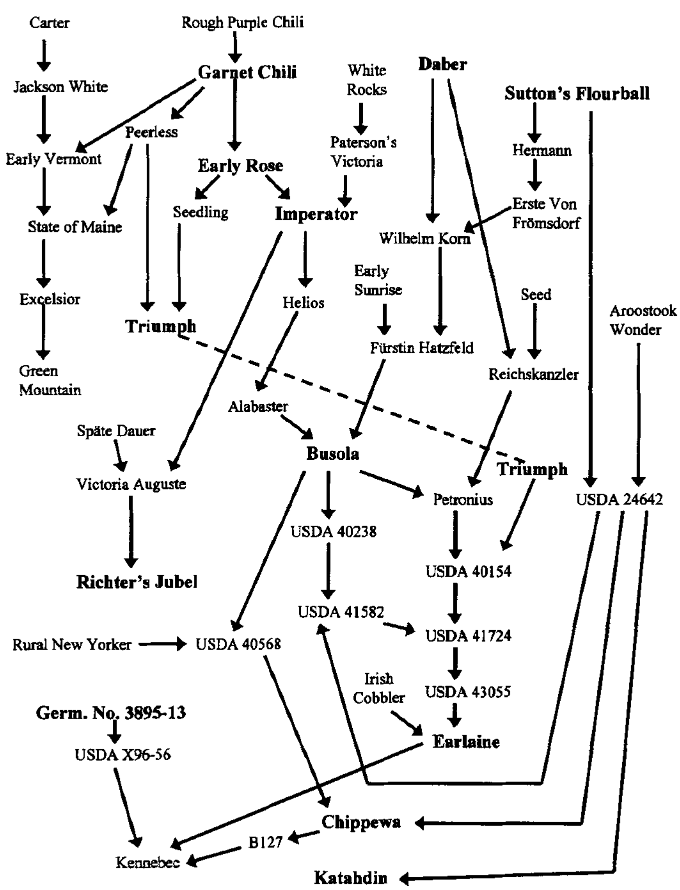

FIGURE 1.
Interrelationship of founding potato clones, major contributing ancestors (MCAs), and selected descendants. MCAs are in bold print.

USDA Beltsville program was the earliest federal breeding program in North America and became the source of much of the germplasm used for cultivar development by later US and Canadian breeders.

Several clones showed up in the pedigrees of numerous prominent cultivars but were not included among the MCAs. The most important of these were Rough Purple Chili, Peerless, Irish Cobbler, and Western Red. Rough Purple Chili was found to be in the ancestry of 100% of the cultivars, Peerless in the ancestry 75%, Irish Cobbler in 70%, and Western Red in 50%. All three were excluded from the major contributing ancestor category because they passed their genes predominately through a single descendant, Rough Purple Chili through Garnet Chili, Peerless through Triumph, Irish Cobbler through Earlaine, and Western Red through Jersey Peachblow. Because the three descendants of Rough Purple Chili, Triumph, and Irish Cobbler were considered MCAs, the contributions of these excluded clones was accounted for.

Three other clones were not considered as major contributors because they were in the ancestry of less than half of the prominent cultivars. However, these clones, Early Gem, B5141-6 (Lenape), and Pontiac, contributed heavily to cultivars within certain market classes. Early Gem was found in the pedigree of all prominent russets except Krantz. Lenape was an ancestor of all prominent chipping cultivars released after 1970 except AC Novachip, Itasca, Kanona, and NorWis. Pontiac was an important contributor to most red cultivars as well as to many of the modern russets.

The number of times each MCA appeared in the pedigree of each cultivar is shown in Table 5. For individual cultivars, these values could be very high. For example, Busola appeared in the pedigree of NorDonna 94 times, Goldrush 82 times, and Conestoga 66 times. Early Rose appeared in the pedigree of Goldrush 93 times, NorDonna 79 times, and CalWhite 66 times. Sutton's Flourball was documented 91, 69, and 60 times in the pedigrees of NorDonna, Goldrush, and Conestoga, respectively. On average, the MCAs appeared in the known 12 generation pedigrees of prominent cultivars in the range of from 4 (Chippewa and Germ. No. 3895-13) to 26 (Early Rose) times.

TABLE 5.—*Number of appearances of each major contributing ancestor in the pedigrees of 44 prominent potato varieties.*

Variety	Busola	Chippewa	Daber	Earlaine	Early Rose	Garnet Chili	Germ. No. 3895-13	Imperator	Katahdin	Richter's Jubel	Sutton's Flourball	Triumph
AC Novachip	20	1	22	3	31	31	1	21	7	4	21	5
Andover	22	4	12	4	11	10	3	14	6	4	22	3
Atlantic	17	3	16	3	15	12	2	16	4	3	18	3
CalWhite	42	7	11	12	66	67	8	21	17	12	34	13
Cascade	5	0	5	0	12	9	0	6	3	1	6	0
Centennial Russet	27	1	22	7	23	24	4	18	4	4	18	7
Century Russet	47	4	28	8	60	57	1	21	19	3	39	13
Chieftain	15	2	15	2	13	15	1	14	7	1	19	3
Chipeta	47	8	23	9	51	46	9	32	10	14	37	9
Conestoga	66	11	22	11	28	24	5	27	35	7	60	14
Frontier Russet	55	3	18	15	32	34	9	24	13	12	38	15
Goldrush	82	10	11	32	93	73	18	31	35	24	69	25
Itasca	62	10	10	28	45	31	20	23	36	16	59	21
Kanona	1	0	6	0	3	3	0	3	1	0	6	0
Katahdin	1	0	1	0	1	1	0	1	0	0	2	0
Kennebec	5	1	6	1	6	7	1	5	1	0	8	1
Krantz	23	1	6	6	21	17	4	7	8	2	20	7
LaChipper	1	0	1	0	3	5	0	2	1	1	3	0
LaRouge	14	2	14	2	12	18	0	12	6	0	20	4
Mainestay	21	3	13	7	8	7	4	13	5	3	19	5
Monona	4	2	4	0	4	4	0	4	2	0	8	0
Nooksack	12	1	17	3	16	17	2	15	1	3	12	3
Norchip	12	4	13	0	12	10	0	16	9	3	21	0
NorDonna	94	28	9	30	79	72	19	42	67	40	91	35
Norland	6	2	6	0	28	38	0	8	4	2	12	2
NorValley	63	17	11	21	41	29	13	26	69	21	63	20
NorWis	10	2	11	1	10	9	0	10	4	0	17	1
Onaway	4	0	5	1	5	6	1	4	1	0	6	1
Ontario	2	1	2	0	3	3	0	3	1	1	4	0
Pike	22	4	12	4	11	10	3	14	6	4	22	4
Ranger Russet	39	7	42	5	53	42	1	40	11	7	32	9
Red LaSoda	1	0	1	0	2	3	0	1	1	0	2	1
Red Pontiac	1	0	1	0	2	3	0	1	1	0	2	1
Red Ruby	32	8	13	5	28	26	4	24	14	12	31	6
Russet Burbank	0	0	0	0	1	1	0	0	0	0	0	0
Russet Norkotah	66	5	22	18	64	57	8	30	15	12	42	21
Russet Nugget	53	5	16	15	47	39	10	24	14	10	39	17
Sangre	28	3	28	4	44	39	0	24	13	2	26	7
Sebago	2	1	2	0	2	2	0	2	1	0	4	0
Shepody	8	1	10	1	23	24	1	10	4	2	12	1
Snowden	35	7	22	6	50	36	7	29	9	11	30	6
Superior	3	0	4	1	41	42	1	4	0	1	4	1
Viking	17	2	19	2	19	14	0	18	9	1	20	3
Yukon Gold	11	2	11	0	11	7	0	11	9	0	18	0
Avg.	25	4	12	6	26	23	4	15	11	6	23	7

Across all 44 prominent cultivars, the genetic contribution of founding clones ranged from 1.5% (Daber) to 23.4% (Katahdin) (Table 6). Katahdin is the immediate parent of four cultivars, including Onaway, Red LaSoda, Red Pontiac, and Sebago, resulting in a 50% genetic contribution for those cultivars. Genetic contribution is a product of both the number of times a clone appears in a pedigree and the number of generations it is removed from the cultivar in question. Clones such as Daber, Early Rose, Garnet Chili, and Imperator tended to show up in pedigrees frequently, but were many generations removed, with subsequently low genetic contributions. Clones such as Chippewa and Earlaine tended to appear recently in pedigrees and had relatively large genetic contributions when compared with the number of appearances. Katahdin tended to be both a recent ancestor and to appear numerous times. The result was a remarkable average genetic contribution of 23.4%. It appears this one clone is responsible for almost one-fourth of the germplasm that makes up prominent North American cultivars. For some cultivars, the total genetic contribution of all MCAs sur-

TABLE 6.—Genetic contribution (%) *of each major contributing ancestor to 44 prominent potato varieties.*

Variety	Busola	Chippewa	Daber	Earlaine	Early Rose	Garnet Chili	Germ. No. 3895-13	Imperator	Katahdin	Richter's Jubel	Sutton's Flourball	Triumph
AC Novachip	14.3	1.6	2.3	18.8	4.8	4.3	6.3	4.0	35.9	9.4	11.8	8.2
Andover	7.9	2.1	1.0	9.0	1.0	0.6	2.7	2.0	20.9	4.3	8.8	0.5
Atlantic	12.5	3.9	1.8	17.2	2.0	1.2	4.7	3.5	28.9	7.8	13.5	1.1
CalWhite	4.8	6.0	0.4	7.4	11.7	9.3	3.0	4.3	9.3	15.7	5.0	1.6
Cascade	10.5	0.0	1.3	0.0	3.0	1.5	0.0	1.4	39.1	0.4	10.1	0.0
Centennial Russet	7.6	6.3	1.2	21.9	5.0	3.1	10.2	5.5	10.2	6.2	7.2	1.4
Century Russet	8.6	4.7	2.2	12.5	15.7	9.9	1.6	3.1	21.9	4.7	8.2	5.5
Chieftain	10.3	4.7	1.4	6.2	4.2	8.4	3.1	2.1	32.8	3.1	13.2	12.9
Chipeta	7.4	7.8	0.9	15.6	6.3	4.6	11.7	7.5	10.2	21.1	9.3	1.0
Conestoga	8.3	7.0	0.9	14.0	2.5	1.6	3.0	2.3	13.5	5.7	7.9	2.1
Frontier Russet	5.8	4.0	0.6	16.7	9.4	8.1	8.5	3.6	8.4	6.4	5.3	1.4
Goldrush	5.6	4.9	0.3	14.0	12.1	7.8	5.7	4.2	10.4	13.0	5.7	2.3
Itasca	6.5	4.1	0.6	6.7	2.2	1.7	3.8	1.6	19.1	4.1	7.0	3.6
Kanona	6.3	0.0	2.0	0.0	0.8	0.4	0.0	1.6	25.0	0.0	6.7	0.0
Katahdin	25.0	0.0	3.1	0.0	1.6	0.8	0.0	3.1	0.0	0.0	25.8	0.0
Kennebec	16.4	25.0	2.4	25.0	1.4	1.1	25.0	2.1	25.0	0.0	14.6	1.6
Krantz	3.4	1.0	0.3	4.5	1.0	0.8	1.8	0.6	11.0	1.0	4.3	1.1
LaChipper	6.3	0.0	0.8	0.0	8.2	10.4	0.0	3.9	25.0	12.5	8.0	0.0
LaRouge	11.9	6.3	1.6	6.3	7.0	16.1	0.0	1.5	37.5	0.0	11.8	25.4
Mainestay	4.8	1.6	1.0	10.1	0.7	0.4	2.8	1.3	8.6	3.2	4.7	0.6
Monona	25.0	50.0	3.1	0.0	1.6	0.8	0.0	3.1	50.0	0.0	25.8	0.0
Nooksack	10.8	12.5	2.0	28.1	8.5	4.7	15.6	9.9	12.5	9.4	8.5	1.8
Norchip	6.2	12.5	0.9	0.0	1.6	0.8	0.0	3.2	15.6	9.4	6.8	0.0
NorDonna	6.8	4.8	0.3	7.4	5.9	6.7	3.8	2.9	20.7	10.7	7.4	11.5
Norland	7.8	6.3	1.0	0.0	20.8	15.5	0.0	4.1	25.0	12.5	8.1	18.8
NorValley	5.9	8.1	0.4	5.1	2.0	1.4	2.2	2.3	14.0	7.6	6.0	2.6
NorWis	18.9	25.0	2.5	6.3	1.3	0.7	0.0	2.4	43.8	0.0	19.3	0.8
Onaway	16.4	0.0	2.4	25.0	1.4	1.1	25.0	2.1	50.0	0.0	14.6	1.6
Ontario	12.5	25.0	1.6	0.0	7.0	3.5	0.0	14.1	25.0	50.0	12.9	0.0
Pike	7.9	2.1	1.0	9.0	1.0	0.6	2.7	2.0	20.9	4.3	8.8	0.6
Ranger Russet	9.0	7.8	2.7	12.5	11.2	6.3	1.6	6.1	12.5	15.6	10.5	3.1
Red LaSoda	12.5	0.0	1.6	0.0	13.3	19.1	0.0	1.6	50.0	0.0	12.9	50.0
Red Pontiac	12.5	0.0	1.6	0.0	13.3	19.1	0.0	1.6	50.0	0.0	12.9	50.0
Red Ruby	4.6	3.7	0.5	3.3	4.6	4.6	1.5	2.7	12.8	9.0	4.9	6.4
Russet Burbank	0.0	0.0	0.0	0.0	50.0	25.0	0.0	0.0	0.0	0.0	0.0	0.0
Russet Norkotah	7.4	6.3	0.8	20.3	18.6	9.9	7.4	5.4	10.7	9.9	6.2	3.7
Russet Nugget	5.9	4.7	0.6	13.2	7.5	4.0	7.1	3.6	11.0	6.0	5.8	2.0
Sangre	10.9	7.8	1.5	12.5	14.8	10.2	0.0	2.8	28.1	6.3	10.0	8.6
Sebago	25.0	50.0	3.1	0.0	1.6	0.8	0.0	3.1	50.0	0.0	25.8	0.0
Shepody	10.4	3.1	4.5	6.3	7.8	7.1	6.3	4.4	34.4	12.5	10.8	0.4
Snowden	8.8	7.0	1.2	20.3	5.4	2.8	10.2	6.8	9.4	23.4	9.4	1.3
Superior	3.9	0.0	0.9	25.0	11.6	6.2	25.0	3.6	0.0	12.5	1.7	1.6
Viking	14.5	12.5	2.0	12.5	5.0	5.7	0.0	3.4	37.5	6.3	13.6	13.3
Yukon Gold	15.6	12.5	2.0	0.0	1.0	0.4	0.0	2.0	50.0	0.0	16.1	0.0
Avg.	10.1	8.0	1.5	9.4	7.2	5.7	4.6	3.5	23.4	7.4	10.2	5.6

passed 100. This resulted from interrelationships among MCAs which caused redundancy in computed contributions (see Figure 1).

The last analysis was computation of the genetic contribution of all exotic germplasm. For purposes of definition, exotic germplasm was considered to be all wild species or ancestors unlikely to share common lineage with the founding clones. This definition led to the exclusion of cultivars and clones with North American or European origins. The resulting pool of exotic ancestors included accessions of eleven *Solanum* species and subspecies, four South and Central American cultivars, and three accessions with *S. demissum* backgrounds that may or may not be unique from that of Germ. No. 3895-13 (Table 7). A few of these ancestors, including Acc. 25892, Acc. 25949, Acc. 25953, Ru4, Germ. No. 3895-13, and AC25953, have undocumented lineage and are likely not entirely exotic but do have known species backgrounds. They were considered to be exotic for the purposes of this study. Excellent summaries of exotic germplasm used in breeding North American cultivars were given by Hougas and Ross (1956) and again by Plaisted and Hoopes (1989).

Thirty-four of the 44 (a remarkable 77%) prominent North American cultivars had some type of exotic ancestry (Table 8). The other ten cultivars had no identifiable exotic ancestors. Sixteen (36%) cultivars had a genetic contribution of exotic germplasm greater than zero but less than 10% (Table 8). At the other extreme, nine cultivars theoretically derived 25% or more of their genotypes from exotic germplasm. These included Atlantic (31.3%), Conestoga (32.3%), Itasca (26.9%), Kennebec (25%), Krantz (49.5%), Onaway (25%), Russet Nugget (34.1%), Superior (25%), and Yukon Gold (31.3%). Russet Nugget has Krantz as one parent and derives most of its exotic ancestry from that side of the pedigree. Krantz has not only a high percentage of exotic parentage in its background, but an unusual combination of wild species (Tables 7 and 8). This is also true of Conestoga which has an exotic germplasm genetic contribution of 32.3% and within 6 generations includes seven *Solanum* species and subspecies in its ancestry. Additional cultivars with high infusion rates of exotic germplasm included Andover (17.5%), Centennial Russet (15.7%), Chieftan (15.6%), Chipeta (17.8%), Frontier Russet (17.5%), Mainestay (18.0%), Nooksack (16.6%), Pike (19.9%), and Snowden (22.7%).

The infusion of exotic germplasm is a relatively recent phenomenon. The only meaningful infusion of exotic germplasm into prominent varieties released before 1966, evident from the pedigrees, was the use of *S. demissum* for late blight resistance in the late 1930s and 1940s. This breeding effort was widely embraced and resulted in Germ. No. 3895-13 being utilized sufficiently often as a parent to be considered an MCA.

Based on the percent of cultivars as descendants, the most commonly used exotic ancestor was Germ. No. 3895-

TABLE 7.—*Description and origin of exotic germplasm found in pedigrees of prominent North American cultivars.*

Exotic Germplasm	Percent of Prominent Varieties as Descendants	Description and Origin
acl	20	*Solanum acaule* from Peru
adg	25	*Solanum tuberosum* subsp. andigena from Central and South America
chc	18	*Solanum chacoense* from Argentina and Bolivia
dem	20	*Solanum demissum* from Mexico (sources other than those listed elsewhere)
ktz	2	*Solanum kurtzianum* from Argentina
mag	2	*Solanum maglia* from Chile
phu	14	*Solanum phureja* from Bolivia, Columbia, and Peru
rap	7	*Solanum raphanifolium* from Peru
sim	2	*Solanum simplicifolium* from Argentina and Bolivia
spg	7	*Solanum spegazzinii* from Argentina
stn	2	*Solanum stenotomum* from Bolivia and Peru
tor	2	*Solanum toralapanum* from Argentina and Bolivia
Acc. 25892	5	A USDA accession of Mexican derived *S. demissum*
Acc. 25949	11	A USDA accession from the Max Planck Institute (Germany) derived from *S. tuberosum* and *S. demissum*
Acc. 25953	2	A USDA accession from the Max Planck Institute (Germany) derived from *S. tuberosum*, *S. tuberosum* subsp. andigena, and *S. demissum*
Ru4	2	A German (Rudorf) seedling with *S. demissum* and *S. tuberosum* ancestry. Imported into Mexico by Neiderhauser. Around 1960 this seedling or its hybrid with Katahdin was imported as Acc. 26055 into the US by USDA breeders
Costa Rican Cultivar	18	An unnamed seedling from Central America (Plaisted and Hoopes, 1989)
SA 327	18	An unnamed South American cultivar (Reeves et al., 1980)
Villaroela	48	A cultivar imported into the US from Chili (Plaisted and Hoopes, 1989)
Yema de Huevo	7	A South American cultivar imported into the US from the International Potato Center (GRIN database)
Germ. No. 3895-13	61	(See Table 2)

TABLE 8.—*Genetic contribution of all exotic germplasm to each of 44 prominent cultivars.*

Cultivar	Genetic Contribution[1] (%)	Exotic Germplasm (# times in pedigree)[2]
AC Novachip	6.3*	G (1)
Andover	17.5*	adg (2), chc (1), V (4), G (3)
Atlantic	31.3*	adg (1), chc (1), V (2), SA (2), CRV (1), G (2)
CalWhite	5.7*	adg (8), dms (8), Acc. 25949 (1), V (10), G (8)
Cascade	6.3	adg (1), dms (8)
Centennial Russet	15.7*	adg (1), dms (16), V (6), G (4)
Century Russet	3.9*	acl (2), V (2), G (1)
Chieftain	15.6*	acl (1), V (2), G (1)
Chipeta	17.8*	chc (1), dms (8), CRV (1), SA (2), V (4), G (9)
Conestoga	32.3*	phu (1), adg (1), chc (2), tor (1), stn (1), sim (1), ktz (1), acl (6), CRV (2), SA (4), V (2), G (5)
Frontier Russet	17.5*	adg (1), dms (2), Acc. 25949 (1), V (8), G (9)
Goldrush	8.2*	adg (1), Acc. 25949 (1), V (24), G (18)
Itasca	26.9*	mag (1), dem (9), adg (1), spg (1), rap (1), phu (1), Acc. 25892 (1), Acc. 25949 (1), YDH (1), V (20), G (20)
Kanona	6.3	adg (1)
Katahdin	0.0	None
Kennebec	25.0*	G (1)
Krantz	49.5*	spg (1), rap (1), phu (1), Acc. 25949 (1), V (10), YDH (1), G (4)
LaChipper	0.0	None
LaRouge	0.0	None
Mainestay	18.0*	Acc. 25953 (1), chc (1), Ru-4 (1), CRV (1), SA (2), V (2), G (4)
Monona	0.0	None
Nooksack	16.6*	dem (8), G (2)
Norchip	3.2	acl (2)
NorDonna	6.1*	acl (1), V (12), G (19)
Norland	0.0	None
NorValley	9.2*	acl (6), chc (1), phu (2), Acc. 25892 (1), CRV (1), SA (2), V (6), G (13)
NorWis	2.3	SA (2), CRV (1)
Onaway	25.0*	G (1)
Ontario	0.0	None
Pike	19.9*	adg (2), chc (1), CRV (1), SA (2), V (4), G (3)
Ranger Russet	7.9*	V (4), G (1)
Red LaSoda	0.0	None
Red Pontiac	0.0	None
Red Ruby	2.3*	V (2), G (4)
Russet Burbank	0.0	None
Russet Norkotah	8.6*	dem (1), V (6), G (8)
Russet Nugget	34.1*	spg (1), rap (1), phu (1), V (12), YDH (1), G (10)
Sangre	3.1	acl (2)
Sebago	0.0	None
Shepody	6.3*	G (1)
Snowden	22.7*	chc (1), SA (2), CRV (1), V (4), G (7)
Superior	25.0*	G (1)
Viking	6.3	acl (2)
Yukon Gold	31.3	phu (1), acl (2)

[1]Genetic contribution percentages accompanied by an * are overestimates due to the presence of unknown S. tuberosum parentage in one or more exotic ancestors. Calculations were made from ancestors within 12 generations.
[2]See Table 6 for an explanation of origins of exotic germplasm. Numbers in parentheses give the number of generations from the prominent cultivar to the exotic ancestor. Abbreviations: G = Germ. No. 3895-13, CRV = Costa Rican Cultivar, SA = SA327, V = Villaroela, and YDH = Yema de Huevo.

13, an *S. demissum* derivation. This clone was present in 61% of the prominent cultivars. Sixty-four percent of the cultivars had *S. demissum* ancestry from one source or another. Other common exotic ancestors included Villaroela, *S. tuberosum* subsp. *andigena*, *S. acaule*, *S. chacoense*, a Costa Rican cultivar, an unnamed South American cultivar (SA 327), and *S. phureja*, present in 48, 25, 20, 18, 18, 18, and 14% of the 44 North American cultivars, respectively (Table 7).

Whereas the genetic contribution of the MCAs should be considered a minimum, the genetic contribution of the exotic ancestors should, for three reasons, be considered a maximum. Firstly, the exotic ancestors not directly derived from wild species likely share common lineage with the founding clones and MCAs. This is especially true for Acc. 25892, Acc. 25949, Acc. 25953, Germ. No. 3895-13, and Ru4, all with *S. demissum* backcrossed to *S. tuberosum* an undetermined number of times. Secondly, the nature of potato breeding prevents the gross genetic contribution of exotic parents from reaching its theoretical level. Selection among clonally propagated families derived from crosses with exotic parents tends to favor preservation of the *S. tuberosum* parental genotype. As a result, useful genes from the exotic parents are introgressed, but the gross genetic contribution of the exotic parent is diminished below computed levels. Thirdly, only a small portion of the actual pedigree of each cultivar is known and the unknown portion is likely all *S. tuberosum*, closely related to the MCA's and founding clones.

One assumption made in most computations of genetic relatedness is that dead-end (those with unknown parentage) ancestors in a pedigree are unrelated (Glendinning, 1997). The most common dead-end ancestors identified in this study were Aroostook Wonder, Sutton's Flourball, Daber, Irish Cobbler, Rough Purple Chili, Rural New Yorker #2, Early Sunrise, Lookout Mountain, White Rocks, Carter, and several other old cultivars. By assumption, these ancestors are considered to be unrelated. However, this assumption is inaccurate (Glendinning, 1997; Hawkes, 1979). As an example, Aroostook Wonder, Irish Cobbler, Rural New Yorker #2, Lookout Mountain, Carter, and possibly Early Sunrise (identity somewhat uncertain) were developed during the period 1860-1900 when it was common practice in the US to develop new cultivars by selecting among open pollinated seedlings for the purpose of circumventing a problem known as "running out". This practice reach its peak following the introduction of Goodrich's Rough Purple Chili, and most cultivars developed during this time were derived, at least in part, from this source (Plaisted and Hoopes, 1989; Stuart, 1929). Evidence for this statement comes from the documented parentage of large numbers of cultivars that came out of this same period. The vast majority have as one parent Garnet Chili, Early Rose, or one of the other Rough Purple Chili derivatives. There is some evidence that Aroostook Wonder is identical to the modern White Rose (Folsom, 1945; Clark and Lombard, 1951). If so, it is undoubtedly a descendant of Rough Purple Chili. It is also likely that the dead-end ancestors of European origin are interrelated (Glendinning, 1983). Regardless, even when no relationship can be inferred from historical evidence, the gene base of these early founding clones undoubtedly had their roots within the germplasm derived from the four introduction events described in the beginning of this paper.

The result of the interrelatedness, in combination with the large proportion of most pedigrees which are unknown, is that inbreeding, coancestry, and genetic contribution coefficients are grossly underestimated. Except for the infusions of exotic germplasm documented in Tables 7 and 8, there is no evidence from the pedigrees that significant proportions of germplasm in prominent cultivars has any source other than the 20 founding clones and 12 MCAs. The interrelationships among the MCAs (Figure 1) contributes further to inbreeding with its potential to reduce the gene base.

The higher genetic contribution of exotic germplasm in newer cultivars indicates that many breeders are successfully expanding the gene base. This is important from the standpoint of improved pest and disease resistance, improved yield potential, and introduction of important novel traits (Horsfall, 1972; Mendoza and Haynes, 1974; Plaisted and Hoopes, 1989). All prominent North American cultivars released since 1965 have some exotic ancestry. However, because the crop was domesticated using only four introductions and most of the gene base is a result of clones derived from those introductions, the gene base is still remarkably narrow. Expansion of this base in potatoes has only just begun and will require purposeful, unwavering efforts by breeders.

ACKNOWLEDGMENTS

The author thanks Dr. Kathy Haynes, USDA, Beltsville, MD, for her assistance in collecting pedigree and clone source information.

LITERATURE CITED

Akeley, R.V., F.J. Stevenson, and E.S. Schultz. 1948. Kennebec: a new potato cultivar resistant to late blight, mild mosaic, and net necrosis. Am Potato J 25:351-361.

Chase, R.W. 1984. North American potato cultivar inventory. Potato Association of America, Orono, Maine.

Clark, C.F. and P.M. Lombard. 1951. Description of and key to American potato cultivars. United States Dept. of Agric. Circ. No. 741.

Darling, H.M. 1959. North American Potato Cultivars. *In:* Potato Handbook. Potato Association of America, Orono, Maine.

Folsom, D. 1945. Potato cultivars: the newly named, the commercial, and some that are useful in breeding. Am Potato J 22:229-242.

Glendinning, D.R. 1983. Potato introductions and breeding up to the early 20th century. New Phytol 94:479-505.

Glendinning, D.R. 1997. Estimation of inbreeding in potato pedigrees. Potato Res 40:277-284.

Hawkes, J.G. 1979. Genetic poverty of the potato in Europe. Proc. Conf. Broadening Genet. Base Crops, Wageningen, 1978. Pudoc, Wageningen.

Horsfall, J.R. 1972. Genetic vulnerability of major crops. Nat Acad Sci Washington, DC, p. 190-203.

Hougas, R.W. and R.W. Ross. 1956. The use of foreign introductions in breeding American potato cultivars. Am Potato J 33:328-339.

Inglis, D.A., D.A. Johnson, D.E. Legard, W.E. Fry, and P.B. Hamm. 1996. Relative resistance of potato clones in response to new and old populations of *Phytophthora infestans*. Plant Dis 80:575-578.

Lansari, A., D.E. Kester, and A.F. Iezzone. 1994. Inbreeding, coancestry, and founding clones of almonds of California, Mediterranean Shores, and Russia. J Amer Soc Hort Sci 119:1279-1285.

Mendoza, H.A. and F.L. Haynes. 1974. Genetic relationships among potato cultivars grown in the United States. HortScience 9:328-330.

National Potato Council. 1997. Potato Statistical Yearbook. Englewood, Colorado.

Plaisted, R.L. and R.W. Hoopes. 1989. The past record and future prospects for the use of exotic potato germplasm. Am Potato J 66:603-627.

Rathlef, H.V. 1932. Die stammtafeln de weltsortiments der Kartoffel und ihre generativ fruchtbaren sorten. Arbeiten aus den Landwirtschaftlichen Instituten der Universitat Halle, Vol. 33:296-431. Paul Parey, Berlin.

Reeves, A.F., R.E. Webb, D.C. Merriam, H.J. Murphy, F.E. Manzer, and P.H. True. 1980. Delta Gold: a new potato cultivar with yellow flesh, high solids, and high quality for baking and processing. Am Potato J 57:429-433.

Salaman, R.N. 1926. Potato cultivars. Cambridge University Press, London, p. 11.

Stevenson, F.J. and C.F. Clark. 1937. Breeding and genetics in potato improvement. *In:* 1937 Yearbook of Agriculture. United States Government Printing Office, Washington, DC.

Stuart, W. 1915. Group classification and varietal descriptions of some American potatoes. United States Dept. Agric. Bull. No. 176.

Stuart, W. 1929. An historical resume of the development of the potato since its discovery. Potato Assoc of Amer Annual Rept.

Swiezynski, K.M., K.G. Haynes, R.C.B. Hutten, M.T. Sieczka, P. Watts, and E. Zimnock-Guzowska. 1997. Pedigree of European and North American potato cultivars. Plant Breeding and Seed Sci 41(Suppl.):1-149.