Table 1.1. *Continued*

Release	Year	Attributes
81-1252-C-2-1-1M	1995	Very late flowering, *ef-1ef-1 ef-2ef-2*
87-1413-2M	1995	Very early flowering, backcrossed to 'Salinas', lettuce
86-197-2-1-4M	1995	Early flowering, backcrossed to 'Prizehead', anthocyanin, lettuce mosaic virus resistance, leaf type
87-20M	1995	Very early flowering, has alleles for pale flowers (*papa*) and salmon flower (*sasa*), butterhead type
87-38M	1995	Very early flowering, has alleles for virescent (*vivi*) and fringed leaf (*frfr*)
87-41M	1995	Very early flowering, has alleles for endive-like leaf (*enen*)
87-42M	1995	Very early flowering, has alleles for chlorophyll deficient-4 (*cd-4cd-4*)
Tiber	1995	Tipburn resistance
87-714-1M	1998	Similar to 'Tiber'
87-714-4M	1998	Similar to 'Tiber'
87-714-5M	1998	Similar to 'Tiber'
87-714-7M	1998	Similar to 'Tiber'
87-715-1M	1998	Similar to 'Tiber'
87-715-2M	1998	Similar to 'Tiber'
87-716-1M	1998	Similar to 'Tiber'
87-716-2M	1998	Similar to 'Tiber'

2

Potato Breeding via Ploidy Manipulations*

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*This paper is dedicated to Emeritus Campbell-Bascom Professor Stanley J. Peloquin, Departments of Genetics and Horticulture at the University of Wisconsin-Madison, whose devotion to and enthusiasm for potato breeding and genetics with 24-chromosome *Solanum* species, haploids, 2*n* gametes and EBN, inspired the author to write this review

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I. INTRODUCTION

Potato is an Andean tuber crop (*Solanum tuberosum* L.) that was originally domesticated in South America, and started its worldwide dissemination after Columbus's voyages. Today, potato is one of the 10 most important crops, and the most important staple starchy food in the world (Table 2.1). Potato yields on average more food energy and protein per unit of land than cereals (Horton 1988). Furthermore, the lysine content of potato can complement cereal-based diets that are deficient in this aminoacid. The plant explorer and geneticist Jack R. Harlan (1995) wrote: "One can more or less live on potatoes if one eats enough of them. A little supplementation with fish, meat, fresh vegetables or dairy products can make a subsistence diet." The impact of potato in terms of changing human history can be demonstrated, among other cases, by the development of the Inca Empire or by the devastation of the Irish famine in the 1840s (Hobhouse 1985; Rhoades 1994).

Potato is not only an important food consumed both fresh and processed, but is also the raw material for the starch-processing industry. Furthermore, potato vines may be used to feed animals, and true

Table 2.1. *The 30 most important crops according to 1995 world total production (http://apps.fao.org/lim500/nph-wrap.pl?Production. Crops.Primary&Domain=SUA).*

Crops	Developed World			Developing World			Total		
	Area (000 ha)	Production[z] (000 t)	Yield (t/ha)	Area (000 ha)	Production[z] (000 t)	Yield (t/ha)	Area (000 ha)	Production[z] (000 t)	Yield (t/ha)
Sugar cane[y]	1,077	84,047	78.1	17,320	1,083,489	62.6	18,398	1,167,535	63.5
Rice	4,368	25,670	5.9	145,197	525,198	3.6	149,566	550,869	3.7
Wheat	119,282	288,907	2.4	100,868	255,408	2.5	220,150	544,315	2.5
Maize	44,082	263,329	6.0	91,588	251,381	2.7	135,670	514,710	3.8
Potato	11,092	182,744	16.5	7,335	102,366	14.0	18,427	285,100	15.5
Sugar beet[y]	6,459	224,815	34.8	1,391	40,006	28.8	7,851	264,821	33.7
Cassava	0	0		16,304	164,163	10.1	16,304	164,163	10.1
Barley	52,095	116,192	2.2	17,309	26,343	1.5	69,404	142,535	2.0
Sweet potato	101	1,919	18.9	9,011	134,222	14.9	9,113	136,141	14.9
Soybean	26,916	63,378	2.4	35,389	62,433	1.8	62,305	125,812	2.0
Banana/Plantain		860			83,787			84,647	
Tomato	1,003	35,443	35.3	2,067	48,945	23.7	3,070	84,389	27.5
Cottonseed	10,014	18,621	1.9	25,338	39,307	1.6	35,352	57,928	1.6
Orange		17,545			39,699			57,243	
Grape		38,186			17,179			55,364	
Sorghum	4,370	13,821	3.2	38,090	40,606	1.1	42,461	54,428	1.3
Apple		24,236			25,577			49,813	
Coconut	0	0		10,102	47,126	4.7	10,102	47,126	4.7
Cabbage	840	20,859	24.8	1109	25,558	23.1	1,949	46,416	23.8
Watermelon	662	8,688	13.1	1,694	31,636	18.7	2,356	40,324	17.1
Dry onion	596	12,165	20.4	1,653	24,916	15.1	2,250	37,081	16.4
Canola	10,152	18,091	1.8	13,394	16,418	1.2	24,146	34,509	1.4
Yam	10	201	20.4	3,164	32,880	10.4	3,174	33,081	10.4
Oat	16,921	27,002	1.6	1,224	1,792	1.5	18,145	28,794	1.6
Peanut	780	1,789	2.3	21,383	26,851	1.3	22,163	28,640	1.3
Millet	1,296	1,051	0.8	34,960	25,949	0.7	36,256	27,000	0.7
Sunflower	13,357	16,198	1.2	7,644	10,079	1.3	21,002	26,277	1.2
Rye	9,727	21,662	2.2	716	1,010	1.4	10,443	22,672	2.2
Mango		78			18,916			18,994	
Dry bean	1,685	2,499	1.5	25,445	15,603	0.6	27,129	18,102	0.7

[z]Total harvested weight.

[y]All crop harvested that is mostly used for the production of centrifugal and non-centrifugal sugar. However, in several countries sugar cane may be used also for seed, feed, fresh consumption, and alcohol. Similarly, some sugar beet may be used for feed and alcohol.

potato seeds contain compounds that have medical applications. World production of potato is estimated at 285 million tonnes, about two-thirds of which is in the industrial countries (Table 2.1). Potato was introduced into North America from Europe at the end of the 17th Century (Plaisted and Hoopes 1989). Today, potato is the leading vegetable crop in the United States. About 0.6 million ha have been grown during the 1990s, with average farm yields in excess of 39 t/ha, and an approximate value of U.S. $2.5 billion. The best U.S. farmers have recorded tuber yields in excess of 67 t/ha (Fageria 1992). The highest national average fresh tuber yield has been recorded in the Netherlands (44 t/ha), although the potential tuber yield of a potato ideotype may exceed 100 t/ha in long-day temperate climates (Evans 1993). Conversely, about 10 t/ha is the national average tuber yield of potato in Perú, which shows that higher yields are achieved outside the area of the origin of this crop.

Potato cultivars in modern high-input agricultural systems are homogeneous tetraploid genotypes. These cultivars, which are generally produced by cross pollination, show a great uniformity due to vegetative propagation by tubers. In this agricultural system, tubers are harvested from a potato plant that grew from a single-sprouted tuber. True seed appears as an alternative for potato production in areas where healthy seed-tubers are not available. In this alternative system, potato tubers are harvested from plants derived from true seed. However, true potato seed cultivars are heterogeneous collections of genotypes derived often from the cross of at least two heterozygous parents. One solution for this potential problem is to select parents for mating schemes with the goal of producing relatively phenotypically homogeneous true seed cultivars (Ortiz 1997). Hence, new true potato seed cultivars should have high underground tuber yield and quality, plus an acceptable aboveground seed yield harvested from the fruit (*see* Section VE).

Potato breeding in the United States benefited dramatically in its early years from the introduction of exotic germplasm (Plaisted and Hoopes 1989). 'Rough Purple Chili' could be one of the most important plant introductions in the genetic betterment of cultivated potato. Tubers of this cultivar were sent from Chile via the U.S. consulate in Panama in 1851, and one seedling arising from open-pollinated seed, later named 'Garnet Chili', was selected by Rev. C. E. Goodrich in Utica, New York. 'Garnet Chili' became the parental source of 'Early Rose', selected by Albert Breese in 1861. 'Early Rose' was the maternal parent of Luther Burbank's famous early potato selection in his mother's potato patch. 'Burbank' was released as a new potato cultivar in 1876. The russet sport of this selection, known as 'Russet Burbank', was released in 1914, and in the early 1990s this cultivar was grown in 40% of the North

American potato area (Plaisted and Hoopes 1989). This story shows that the North American principal potato cultivar resulted from three generations of selection and recombination, through outcrossing in respective open-pollinated generations from the original plant introduction (Douches et al. 1991).

Most potato cultivars are closely related because a few parents are repeated in their pedigree (Plaisted and Hoopes, 1989). This could explain why the genetic yield potential of potato in North America has not improved despite the breeding efforts and release of new cultivars in the twentieth century (Douches et al. 1996). Hence, genes from wild *Solanum* species are being transferred into the tetraploid potato breeding pool to broaden its genetic base. In addition, alleles for pest and disease resistance to major biotic stresses may alleviate the chemical pesticide dependency associated with potato cultivation. Resistant potato cultivars allow environmental conservation and diminish costs on high-input potato farms. The potato crop offers a good example that for some crops alleles from wild species may be required for their further genetic improvement (Harlan 1976).

Tarn et al. (1992) discussed the advances in breeding potatoes for long-day temperate climates that had taken place up until the late 1980s. Their review focused on strategies for cultivar development, with a brief discussion of ploidy manipulations. Our paper reviews in depth the last ten years of ploidy manipulations for the introgression and incorporation of *Solanum* genetic resources into the cultivated gene pool. Other molecular and cellular approaches for gene introgression from wild species were explained recently by Hermsen (1994).

II. THE ANALYTICAL BREEDING SCHEME AND ITS COMPONENTS

An analytical scheme for potato breeding was first proposed by Chase (1963). In this approach, tetraploid potato cultivars are "reduced" to the diploid level by producing haploids. To avoid confusion, haploids of the cultivated potato are defined in this review as sporophytes with the gametic chromosome number, i.e. $2n = 2x = 24$. In other publications, the term dihaploid has been used to refer to haploids of a tetraploid because they are diploid. The term dihaploid was not used in this review because this was the early name for doubled haploids in other crops. In the analytical breeding scheme, haploids are crossed with other diploid stocks for breeding at the diploid level, and tetraploid hybrids are resynthesized via polyploidization.

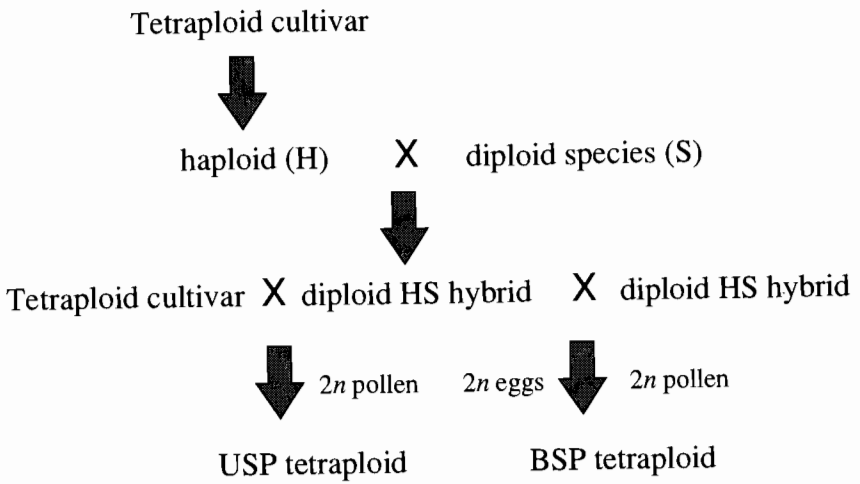

Fig. 2.1. Ploidy manipulations for the improvement of cultivated tetraploid potato with haploids, species, and 2*n* gametes. Maternal haploids are easily obtained from tetraploid cultivars through parthenogenesis. Unilateral sexual poliploidization (USP) or bilateral sexual poliploidization (BSP) tetraploids are developed by 4*x*-2*x* crosses or 2*x*-2*x* crosses due to the occurrence of 2*n* gametes in the diploid parent(s).

Scaling up and down the chromosome sets (i.e., ploidy manipulations) are easily achieved in potato (Peloquin et al. 1989b). Mendiburu and Peloquin (1976, 1977a,b, 1979) and Mendiburu et al. (1974) provided the terminology and scientific framework for the systematic utilization of ploidy manipulations for genetic improvement and analysis of the potato genome (Fig. 2.1). As pointed out by Peloquin and his colleagues of the University of Wisconsin at Madison (1989c): "The potato is unsurpassed in the facility with which sets of chromosomes can be manipulated. This allows a germplasm enhancement strategy that involves species, haploids, 2*n* gametes and endosperm balance number (EBN). The species are the source of genetic diversity, haploids provide a method for 'capturing' the diversity, and 2*n* gametes and EBN are involved in an effective and efficient method of transmitting diversity to cultivars." This approach in potato breeding was reviewed about a decade ago (Peloquin et al. 1989a).

A. *Solanum* Species and Cultivated Potato

Potato is unique among crop plants due to the abundance of related wild species and the easy incorporation of this germplasm into the cultivated gene pool (Peloquin et al. 1989a). Interspecific vigorous fertile

hybrids are obtained through sexual crosses. Chromosome pairing and crossing over between cultivated and wild *Solanum* species occurs normally due to the lack of extensive chromosome differentiation among taxa. Introgression of small chromosome segments (associated with specific characteristics) can be achieved through chromosome engineering in potato. Likewise, after germplasm enhancement with haploids from tetraploid cultivars, many chromosome segments (controlling quantitative characteristics) from wild species can be incorporated into the cultivated tetraploid gene pool via 2*n* gametes.

There are 216 tuber-bearing species and 9 non-tuber bearing species in the genus *Solanum* section *Petota* Dumort (Spooner and Bamberg 1994). An endosperm dosage system, also known as endosperm balance number (EBN) (*see* Section IIE), played an important role in the speciation of polyploid from diploid *Solanum* species (Hawkes and Jackson 1992). Polysomic tetraploid species and all modern tetraploid cultivars are 4 EBN, while disomic tetraploid species are 2 EBN. Free gene flow and no barrier for intraspecific crosses occur between the polysomic tetraploid cultivated potato (4 EBN). Thus, the potato primary gene pool consists of old and modern tetraploid cultivars, tetraploid Andean landraces, and tetraploid breeding populations. Diploid cultivars, breeding populations, and tuber-bearing wild species (2 EBN) producing 2*n* gametes and hexaploid (4 EBN) species also belong to this primary pool. Hence, the potato primary gene pool refers to the biological species of a group since they are supposed to be completely interfertile.

The secondary gene pool consists of those species that are able to exchange genes with the primary pool but after "difficult" interspecific hybridization through introgression. Disomic tetraploid species (2 EBN) and diploid (1 EBN) tuber-bearing *Solanum* species are in this secondary potato gene pool. These species may cross with the crop primary gene pool to provide a source of gene transfer, after isolation barriers (mainly due to EBN) are overcome (*see* Section IIIA).

The tertiary potato gene pool consists of non-tuber bearing diploid wild species (1 EBN) of the series *Etuberosa* Juz. and other *Solanum* species. This tertiary gene pool could cross with the primary gene pool through special techniques such as bridge species and embryo rescue (*see* Section IIIC1). For example, the common weed black nightshade (*Solanum nigrum* L.) is a non-host to the fungus *Phytohpthora infestans* (Mont.) De Bary (late blight), and Dutch potato breeders have considered the transfer of this non-host resistance to new potato cultivars. Eijlander and Stiekema (1994) were able to bridge the crossability gap between disomic hexaploid black nightshade and the tetraploid cultivar 'Desiree' through embryo rescue. Backcrossing this experimental hybrid

to *S. tuberosum* aided by embryo rescue may help to introgress the desired gene(s) to the potato primary gene pool.

Other diploid and tetraploid species from the *S. nigrum* complex are being considered for transfer of resistance to the potato breeding pool. However, interspecific hybrids from crosses between species of the primary and tertiary gene pools may be anomalous, lethal, or completely sterile. Indeed, the hybrids between *S. nigra* and *S. tuberosum* were sterile. Moreover, *S. nigra* could be used only as female in crosses with *S. tuberosum* due to unilateral incompatibility. The flowers of *S. nigra* were also emasculated because its pollen outcompeted potato pollen. The research reported by Eijlander and Stiekema (1994) provides an example that natural gene flow by pollen dispersal from the cultivated potato tetraploid gene pool to *S. nigra* is highly unlikely.

The glycoalkaloid content in tubers changed during domestication of potato (Johns and Alonso 1990). This selection for reduced toxicity during potato domestication created concern among potato breeders for the incorporation of wild *Solanum* genetic resources in their breeding programs. Some wild tuber-bearing *Solanum* species may have high levels (greater than 20 mg/100 g) of glykoalkaloid content in their tubers. However, as shown by practical breeding experience, large variability for glycoalkaloid content was found in the haploid-species hybrids. This result indicated the feasibility of selecting for low glycoalkaloid content in the breeding population.

Specific genes from wild or exotic *Solanum* germplasm have been introgressed into the cultivated tetraploid gene pool to achieve multiple pest and disease resistance (Ross 1986; Plaisted and Hoopes 1989). This explains why many *Solanum* species, especially *S. acaule* Bitt., *S. chacoense* Bitt., *S. demissum* Lindl., *S. spegazzinii* Bitt., *S. stoloniferum* Schechtd. et Bche., and *S. vernei* Bitt. et Wittm., are already present in the pedigrees of modern European and North American cultivars.

1. Collecting Tuber-bearing *Solanum* Diversity. Wild *Solanum* species grow naturally throughout most America: from the southwestern United States to south-central Chile. They occupy a wide number of habitats: from desert to rain forest, from cultivated fields to stony hills and mountains, from sea level to more than 4000 m altitude (Hanneman 1989; Spooner and Bamberg 1994). These wild *Solanum* spp. are the most important source of desired alleles for potato breeding, especially for disease and pest resistance (Hawkes 1990). Also, *Solanum* spp. possess alleles for improving agronomic and quality characteristics. Tuber-bearing *Solanum* spp. show continuous polymorphism for tuber size and taste (Spooner and Bamberg 1994). Tubers range from very small to nearly cultivar size, and from edible and flavorful to bitter and toxic.

Genetic resources from wild *Solanum* spp. become available after extensive well-planned collections. These accessions can be acquired in rural markets, farmers' fields, or remote areas. Over the past ten years, new *Solanum* genetic resources have become available to potato breeders after systematic expeditions to Argentina, Bolivia, Chile, Colombia, Ecuador, Mexico, and Venezuela (Spooner et al., 1991, 1992, 1993, 1994, 1995; Spooner and Clausen 1993; Rodriguez et al. 1995a). Thus, plant exploration and potato gene-banks are broadening the potato germplasm base.

2. Searching for Desired Alleles in Tuber-bearing *Solanum* spp. Screening of the *Solanum* accessions is the starting point for potato breeders to open this hidden genetic treasure. Systematic search of desired alleles in accessions available in gene-banks provides diverse germplasm options for potato breeders interested in developing new breeding populations or cultivars with a broad genetic base. Variation exists between and within accessions of *Solanum* spp. In addition, accessions may be segregating and this could explain inconsistent or even contradictory reports among scientists searching for the same desired alleles. Furthermore, screening methods may account for conflicting reports.

Potato breeders select promising genotypes that combine many desired tuber and processing characteristics, as well as resistance to major pests and diseases (Jellis 1992). Highest priority for potato breeding in the Northern Hemisphere is given to late blight, viruses (potato leaf roll luteovirus and potato virus Y potyvirus), cyst nematode (*Globodera pallida* Stone), golden nematode [*G. rostochiensis* (Woll.)], and insect pests, as well as high dry matter and low reducing sugars in the tubers. Heat and cold tolerance, and resistance to late blight, viruses, bacterial wilt [*Pseudomonas solanacearum* (E.F. Sm.)], cyst and root-knot nematodes (*Meloidogyne* spp.), and potato tuber moth [*Phthorimaea operculella* (Zeller)] are among the most desired characteristics for potato breeding in the tropics. Diverse sources of resistance are available in tuber-bearing and non-tuber bearing *Solanum* spp. (Table 2.2).

Crop protection scientists should agree on signs and symptoms, and common techniques for assessment of specific pests and diseases in the laboratory, glasshouse, and field (natural and artificial infestation). There are early generation screening techniques available to select for multiple resistance and to determine the breeding value of parental sources (Jellis 1992). However, field and laboratory (or glasshouse) screening must be correlated, as well as assessment at early and adult stages. For example, seedling progeny tests in the glasshouse detected the most resistance crosses for potato leaf roll virus, but failed for selection of most resistant genotypes (Solomon-Blackburn et al. 1994).

Any progress in resistance breeding depends on the reliability of the

Table 2.2. Promising *Solanum* species for transfer of desired characteristics to *S. tuberosum* gene pool.

Characteristic	Species[z]	Reference
Accumulation of Ca in tuber[y]	*S. gourlayi, S. microdontum*	Bamberg et al. 1993
Cold tolerance	*S. sanctae-rosae*	Tucci et al. 1996
Foliar glycoalkaloids[y]	Most *Solanum* species have low content	Deahl et al. 1993
Glandular trichomes[y]	*S. berthaultii*	Neal et al. 1989
Frost hardiness[y]	*S. acaule, S. albicans, S. commersonii, S. demissum, S. paucissectum*	Vega and Bamberg 1995
Heat tolerance (tuberization)[y]	*S. bulbocastanum, S. chacoense, S. demissum, S. stoloniferum*	Reynold and Ewing 1989
Lack of enzymic browning	*S. hjertingii*	Gubb et al. 1989
Male fertility under heat stress[y]	*S. kurtzianum, S. megistacrolobum*	Bamberg 1995
2*n* pollen	Almost all tuber-bearing Solanums	Ortiz 1994
Resistance		
Early blight[y] [*Alternaria solani* Sorauer]	*S. acaule, S. canasense, S. multidissectum, S. multiinterruptum, S. pascoense, S. pinnatisectum*	Hanneman 1989
Late blight [*Phytophthora infestans* (Mont.) de Bary]	*S. phureja*	Canizares and Forbes 1995
	S. andigena, S. berthaultii, S. chacoense, S. microdontum, S. sucrense, S. venturii, S. vernei, S. verrucosum	Colon and Budding 1988
	S. berthaultii, S. circaeifolium, S. microdontum, S. sparsipilum, S. sucrense, S. verneii	Colon et al. 1995a
	S. microdontum, S. phureja, S. verrucosum	Swiezynski et al. 1991
Verticillium wilt[y] [*Verticillium dahlae* Kleb.]	*S. berthaultii, S. chacoense, S. sparsipilum, S. tarijense*	Corsini et al. 1988
	S. andigena, S. berthaultii, S. chacoense, S. gourlayi, S. marinasense, S. medians, S. megistacrolobum, S. microdontum, S. multiinterruptum, S. oplocense, S. papita, S. polytrichon, S. raphanifolium, S. sparsipilum, S. sucrense, S. tarijense, S. toralapalum, S. trifidum	Hanneman 1989
Silver scurf[y] [*Clavibacter michiganense* spp. *sepedonicum* (Spleck & Kott.)]	*S. acaule, S. chacoense, S. demissum, S. hondelmanii, S. oxycarpum, S. stoloniferum*	Rodriguez et al. 1995b
Soft rot[y] [*Erwinia* spp.]	*S. andigena, S. berthaultii, S. bulbocastanum, S. chacoense, S. stoloniferum, S. tarijense*	Lojkowska and Kelman 1989
	S. stenotomum - S. phureja	Wolters and Collins 1994
	S. andigena, S. chacoense, S. phureja, S. vernei	Rouselle-Bourgeois and Priou 1995
	S. canasense, S. multidissectum, S. tarijense	Carputo et al. 1996
Ring rot[y]	*S. acaule*	Kriel et al. 1995
Bacterial wilt[y]	*S. acaule, S. chacoense, S. commersonii, S. demissum*	Hanneman 1989
Potato virus X (PVX) (potexvirus)	*S. andigena, S. lesteri, S. marinasense*	Horvath et al. 1988
	S. andigena, S. commersonii, S. oplocense, S. sparsipilum	Tozzini et al. 1991
	PVX[common strain]: *S. phureja - S. stenotomum*	Vallejo et al. 1994c
Potato virus Y (PVY) (potyvirus)	*S. brevidens, S. fernandezianum, S. hermanii, S. trifidum*	Horvath et al. 1988
	S. acaule, S. andigena, S. megistacrolobum, S. stoloniferum	Singh et al. 1994
	PVY[0]: *S. phureja - S. stenotomum*	Vallejo et al. 1994c
Colorado potato beetle[y] [*Leptinotarsa decemlineata* Lay.]	*S. berthaultii, S. chacoense, S. pinnatisectum, S. tarijense*	Bamberg et al. 1996
	S. berthaultii, S. boliviense, S. capsicibaccatum, S. chacoense, S. commersonii, S. jamesii, S. oplocense, S. pinnatisectum, S. polyadenium, S. tarijense, S. trifidum	Flanders et al. 1992, 1997
Green peach aphid[y] [*Myzus persica* Sulzer]	*S. brachistotrichum, S. bulbocastanum, S. canasense, S. etuberosum, S. hertingii, S. infundibuliforme, S. jamesii, S. lignicaule, S. marinasense, S. sanctae-rosae, S. stoloniferum, S. tarijense, S. toralapanum, S. trifidum*	Flanders et al. 1992, 1997
	S. brevidens	Valkonen et al. 1992
Potato aphid[y] [*Macrosiphum euphorbiae* (Thomas)]	*S. albicans, S. bukasovii, S. bulbocastanum, S. chomatophilum, S. demissum, S. hertingii, S. hougasii, S. lignicaule, S. medians, S. multidissectum, S. stoloniferum, S. verrucosum*	Flanders et al. 1992, 1997
Potato flea beetle[y] [*Epitrix* spp.]	*S. alandie, S. berthaultii, S. blanco-galdosii, S. boliviense, S. brachistotrichum, S. bulbocastanum, S. cardiophyllum, S. commersonii, S. immite, S. incamayoense, S. iopetalum, S. marinasense, S. megistacrolobum, S. microdontum, S. mochicense, S. multiinterruptum, S. pampasense, S. pinnatisectum, S. piurae, S. polyadenium, S. sanctae-rosae, S. schickii, S. stoloniferum, S. tarijense, S. toralapanum, S. verneii, S. weberbaueri*	Flanders et al. 1992, 1997

Table 2.2. *Continued*

Characteristic	Species[z]	Reference
Potato leafhopper[y] [*Empoasca fabae* Harris]	*S. berthaultii, S. blanco-galdosii, S. brachistotrichum, S. brachycarpum, S. bulbocastanum, S. cardiophyllum, S. chomatophilum, S. colombianum, S. etuberosum, S. fernandezianum, S. megistacrolobum, S. multiinterruptum, S. oxycarpum, S. polyadenium, S. polytrichon, S. tarijense, S. toralapanum, S. trifidum, S. violaceimarmoratum*	Flanders et al. 1992, 1997
Potato tuber moth [*Phthorimaea operculella* (Zeller)]	*S. commersonii, S. pinnatisectum, S. sparsipilum, S. sucrense, S. tarijense*	Chavez et al. 1988b
Cyst nematode [*Globodera pallida* (Stone)]	PA_1: *S. andigena, S. canasense, S. demissum, S. gourlayi, S. leptophyes, S. megistacrolobum, S. multidissectum, S. sparsipilum, S. spegazzinii, S. sucrense, S. vernei, S. verrucosum*	Dellaert and Hoekstra 1987
	PA_2, PA_3: *S. acaule, S. andigena, S. berthaultii, S. boliviense, S. brevicaule, S. canasense, S. chacoense, S. demissum, S. gourlayi, S. leptophyes, S. megistacrolobum, S. microdontum, S. multidissectum, S. oplocense, S. sparsipilum, S. spegazzinii, S. sucrense, S. vernei, S. verrucosum*	
	PA_4: *S. capsicibaccatum, S. gourlayi, S. leptophyes, S. vernei*	Chavez et al. 1988a
	PA_5: *S. sparsipilum*	
	PA_1: *S. andigena, S. gourlayi, S. kurtzianum, S. megistacrolobum, S. oplocense, S. raphanifolium, S. sanctae-rosae, S. sparsipilum, S. spegazzinii, S. stenotomum, S. sucrense, S. toralapanum*	Turner 1989
	PA_2: *S. acaule, S. andigena, S. kurtzianum, S. sparsipilum, S. spegazzinii, S. stenotomum*	
	PA_3: *S. acaule, S. andigena, S. berthaultii, S. brevicaule, S. goniocalyx, S. gourlayi, S. kurtzianum, S. megistacrolobum, S. oplocense, S. phureja, S. raphanifolium, S. sanctae-rosae, S. sparsipilum, S. spegazzinii, S. stenotomum, S. sucrense, S. toralapanum*	
Golden nematode [*Globodera rostochiensis* (Woll.)]	$PA_{2/3}$: *S. gourlayi, S. sparsipilum, S. spegazzinii, S. vernei*	Rouselle-Bourgeois and Mugniery 1995
	$PA_{1/2/3}$: *S. acaule, S. andigena, S. brevicaule, S. leptophyes, S. sparsipilum, S. sucrense*	Jackson et al. 1988
	Ro_1: *S. acaule, S. andigena, S. berthaultii, S. boliviense, S. brevicaule, S. canasense, S. demissum, S. gourlayi, S. leptophyes, S. megistacrolobum, S. microdontum, S. multiinterruptum, S. sparsipilum, S. spegazzinii, S. sucrense, S. vernei, S. verrucosum*	Dellaert and Hoekstra 1987
	Ro_2: *S. andigena, S. brevicaule, S. canasense, S. megistacrolobum, S. multidissectum, S. spegazzinii, S. sucrense, S. vernei*	
	Ro_3: *S. andigena, S. brevicaule, S. canasense, S. gourlayi, S. megistacrolobum, S. multidissectum, S. spegazzinii, S. sucrense, S. vernei*	
	Ro_5: *S. acaule, S. andigena, S. berthaultii, S. boliviense, S. brevicaule, S. canasense, S. chacoense, S. demissum, S. gourlayi, S. leptophyes, S. megistacrolobum, S. microdontum, S. multiinterruptum, S. oplocense, S. sparsipilum, S. spegazzinii, S. sucrense, S. vernei, S. verrucosum*	
	Ro_1: *S. acaule, S. andigena, S. berthaultii, S. brevicaule, S. gourlayi, S. kurtzianum, S. megistacrolobum, S. microdontum, S. oplocense, S. raphanifolium, S. sanctae-rosae, S. sparsipilum, S. spegazzinni, S. stenotomum, S. sucrense*	Turner 1989
	Ro_2: *S. andigena, S. brevicaule, S. goniocalyx, S. gourlayi, S. kurtzianum, S. megistacrolobum, S. microdontum, S. oplocense, S. raphanifolium, S. sanctae-rosae, S. sparsipilum, S. spegazzinii, S. stenotomum, S. sucrense, S. toralapanum*	
	Ro_3: *S. andigena, S. gourlayi, S. kurtzianum, S. megistacrolobum, S. microdontum, S. oplocense, S. raphanifolium, S. sanctae-rosae, S. sparsipilum, S. spegazzinii, S. stenotomum, S. sucrense*	
	Ro_4: *S. andigena, S. kurtzianum, S. sparsipilum, S. stenotomum*	
	Ro_5: *S. acaule, S. andigena, S. brevicaule, S. gourlayi, S. kurtzianum, S. megistacrolobum, S. oplocense, S. raphanifolium, S. sanctae-rosae, S. sparsipilum, S. spegazzinii, S. stenotomum, S. sucrense, S. toralapanum*	
	Ro_1: *S. andigena, S. gourlayi, S. spegazzinii, S. vernei*	Rouselle-Bourgeois and Mugniery 1995

Table 2.2. *Continued*

Characteristic	Species[z]	Reference
Root knot nematodes [*Meloidogyne* spp.]	*S. acaule*, *S. arnezii*, *S. boliviense*, *S. brachistotrichum*, *S. bulbocastanum*, *S. cardiophyllum*, *S. chacoense*, *S. fendleri*, *S. gourlayi*, *S. hougasii*, *S. microdontum*, *S. sparsipilum*, *S. spegazzinii*, *S. sucrense*	Janssen et al. 1995, 1997
Columbia root knot nematode [*Meloidogyne chitwoodi* Golden, O'Bannon, Santo & Finley]	*S. hougasii*	Brown et al. 1991
	S. bulbocastanum, *S. cardiophyllum*, *S. brachistotrichum*, *S. fendleri*, *S. hougasii*	Janssen et al. 1995, 1997

[z]*S. andigena* Juz. et Buk. is the tetraploid Andean cultivated potato, while *S. phureja*, *S. stenotomum*, and *S. goniocalyx* Juz. et Buk. are diploid cultivars in the Andes. Authority for all *Solanum* species listed in this table is available from Huaman and Ross (1985).

[y]Specific information on resistant plant introductions can be obtained from htpp\\:www.ars-grin.gov/cgi-bin/npgs/html/site.pl?NR6

screening method. Therefore, collaboration of gene-bank curators, crop protection scientists, geneticists, and breeders should ensure the proper utilization of this germplasm for potato improvement. Progress in DNA marker-assisted selection may improve the screening and selection in resistance breeding (*see* Sections IVC1, and VF).

B. Haploids of Cultivated Potato and Wild Species

Scaling down the ploidy of the tetraploids cultivars and breeding materials to the diploid level is achieved routinely by producing potato haploids.

1. Production and Origin. Maternal haploids can be easily obtained through parthenogenesis after interspecific hybridization of tetraploid cultivars with pollen of *S. phureja* Juz. et Buk. (Peloquin et al. 1996). Haploid frequency appears to be affected by both the maternal genotype and the pollen source (Singsit and Hanneman 1991b; Ortiz et al. 1992/1993; Liu and Douches 1993; Hutten et al. 1994b; Peloquin et al. 1996). Also, a significant interaction between seed parent and pollen source occurs for haploid induction and production (Hutten et al. 1994b).

Paternal haploids are also obtained via anther culture (Uhrig and Salamini 1987; Calleberg and Johansson 1993; Rokka et al. 1996). However, maternal haploids offer more advantages for potato breeding because paternal haploid production requires gene(s) for androgenic competence (Singsit and Veilleux 1989; Sonnino et al. 1989; Taylor and Veilleux 1992). These genes are not always available in tetraploid potato cultivars. Furthermore, the ploidy of anther-derived plants varies broadly. Regenerated plants may be haploid, monoploid, mixoploid, or polyploid. Occurrence of $2n$ microspores, nuclear fusion, endoreduplication, and endomitosis, which may occur during the regeneration phase (Pijnacker et al. 1989), underlie ploidy polymorphism of anther-derived potato plantlets. Regeneration of shoots from somatic tissue is another source of ploidy polymorphism.

Maternal haploids are easily identified due to their phenotype or with the aid of markers such as embryo spot (Ortiz et al. 1992/1993) or by electrophoretic analysis (Liu and Douches 1993). A seed selection system combining the absence of the embryo spot with seed diameter greater than 1.25 mm improved the early detection of haploids after $4x$-$2x$ crosses (Caligari et al. 1988). Although genetic or phenotypic markers available in the diploid pollen source but absent in the tetraploid seed parent are useful for early selection of potential maternal haploids, ploidy must be confirmed through chromosome counting from root tips.

Clulow et al. (1993) observed preferential chromosome elimination of

the *S. phureja* genome in some maternal haploids. This phenomenon could give rise to predominantly diploid, aneusomatic individuals containing very low frequency of *S. phureja* chromosomes (Clulow et al. 1991). Molecular markers and in situ hybridization showed that DNA from the pollen source (IvP-48) was incorporated in some haploids by somatic translocation during haploid induction (Waugh et al. 1992; Wilkinson et al. 1995). Likewise, principal component analysis, based on phenotypic characteristics, suggested that IvP-48 may affect the morphology of some putative maternally-derived haploids (Allainguillaume et al. 1997). Conversely, Singsit and Hanneman (1991b) demonstrated the occurrence of pseudogamous parthenogenetic haploid production by manipulating ploidy levels and the EBN (*see* Section IIE). Disomic tetraploid (2 EBN) species from Mexico were chromosome-doubled with colchicine. The resultant octoploids (4 EBN) were crossed with *S. phureja* 1.22, and tetraploid (2 EBN) offspring were obtained. Furthermore, Peloquin et al. (1996) indicated that the endosperm associated with a haploid embryo was always hexaploid. This clearly demonstrated the union of the two chromosome sets of the *S. phureja* with the polar nuclei, and lack of fertilization of the egg. Hence, the pollen source influences haploid frequency via its effect on the endosperm.

2. Genetic Analysis and Improvement with Haploids. Peloquin et al. (1990), and Tellhem and Wersuhn (1990a) reviewed the utilization of haploids for genetic research in potato until the late 1980s. In recent years, investigations with haploids have enabled the determination of the genetic load of the tetraploid parent (Kotch et al. 1992; Hutten et al. 1995b). This genetic load was measured by phenotypic distribution, the recovery of lethal mutants, and the occurrence of genic male sterility. Also, molecular maps of potato have been developed based on populations derived from heterozygous haploids (*see* Section IVC).

Concilio (1992) extracted haploids from a broad-based tetraploid population. Close resemblance to either the tetraploid or wild species grandparents was observed in some haploids. Distorted segregation in the tetraploid populations after two cycles of recombination could explain this finding. De,Maine (1995) investigated the effects on inbreeding in a second haploid generation. Haploids from tetraploid cultivars were chromosome-doubled and maternal haploids were obtained again. Seed set in the second haploid generation was higher than in the original haploid generation, whereas tuber yield was the same. This result demonstrated that most deleterious recessive alleles were unmasked by the original haploid generation. Residual variation within the original haploid generation may be exploited for potato breeding with the second haploid generation.

Solanum acaule is a disomic tetraploid (2 EBN) species showing bivalent pairing at meiosis. Camadro et al. (1992) extracted haploids of this species to investigate their meiotic behavior and electrophoretic pattern. On average, 10.6 univalents and 6.7 bivalents were observed in meiosis. Hence, male fertility was low in these haploids of *S. acaule*. The isozyme analysis showed a fixed heterozygous genotype for homoeologous loci, which did not segregate during meiosis of tetraploid *S. acaule*.

The inbreeding coefficient of maternal haploids depends on the inbreeding and coefficient of coancestry of its tetrasomic polyploid parent, and the coefficient of double reduction (α) for a specific locus (Haynes 1993; Ortiz and Peloquin 1994b). In tetraploids, α ranges from 0 (chromosomal segregation) to 1/6 (maximal equational segregation). When α is greater than zero (far from centromere), the inbreeding coefficient of the haploid should be larger than that of its tetraploid parent (Haynes 1993). However, for a polygenic trait, the inbreeding coefficient of a haploid would be nil because double reduction for those loci seldom occurs. The coefficient of double reduction (α) in the cultivated tetraploid potato was calculated for morphological and isozyme loci using haploids (Haynes and Douches 1993; Ortiz and Peloquin 1994b), and double reduction occurred only sporadically.

Chromosome doubling of haploids was suggested to increase the homozygosity of tetraploid testers (De,Maine and Jervis 1989). The chromosome-doubled haploids (CD-2*x*) could have quadriplex, duplex, or nulliplex genotypes. De,Maine and Fleming (1991) derived the genotype of the tetraploid parent, and elucidated the inheritance of tuber skin pigmentation, tuber flesh color, and skin russeting in offspring derived from crosses between these CD-2*x* and 4*x* parents.

The breeding value of haploids producing 2*n* eggs was evaluated in 2*x*-4*x* crosses (Werner and Peloquin 1991d; De,Maine 1994b). Haploids and their derived CD-2*x* had similar breeding value for yield, and their tetraploid hybrids were as high yielding as hybrids derived from 4*x*-4*x* crosses (De,Maine 1994b). There were no differences between haploids derived from diverse tetraploid cultivars (Werner and Peloquin 1991d). However, haploids from the same tetraploid parent possessed significantly different breeding values, which were unaffected by the mode of 2*n* egg formation. This finding suggested that selection among haploids should be carried out through progeny testing before further utilization in 2*x*-4*x* or 2*x*-2*x* crosses. Haploids should be evaluated with unrelated tetraploid testers to avoid biased results due to inbreeding depression. These results demonstrated that haploids *per se* are not the best parents to develop high-yielding tetraploid hybrids in the analytical breeding scheme, as earlier shown by Maris (1990). High yields in potato are expected from crossing unrelated but adapted materials. This could be

achieved by the development of diploid hybrids (between potato haploids and diploid *Solanum* spp.) that have been locally selected but with a broad genetic base.

The undesirable characteristics of non-adapted *Solanum* species may be reduced by increasing genes of *S. tuberosum* in the breeding population. Haploids derived from tetraploid cultivars are the best female parents for germplasm enhancement of these diploid (2 EBN) wild *Solanum* species (Jansky et al. 1990). Wild species lack tuberization under long days due to absence of photoperiod adaptation, prolonged dormancy, or insufficient growing period for tuberization. Haploid-species hybrids are the remedy to allow the evaluation of tuber characteristics under long day length of non-adapted wild species (Yerk and Peloquin 1989b). However, the breeding value of these haploids may differ in crosses with wild *Solanum* species. Hence, haploid parents should be tested and selected for their utilization in germplasm enhancement at the diploid level (Yerk and Peloquin 1990b).

Most haploids from *S. tuberosum* are female fertile but male sterile. However, haploids show significantly different female fertility that may be influenced by environment (Trognitz 1995). Berry set in haploids depended on the pollen source. Selection for female fertility is required in the early generations to avoid failures on seed set after hybridization.

C. Fertility of Haploid-species Hybrids

Haploid-species hybrids show male sterility when a sensitive cytoplasm (e.g., *S. tuberosum*) interacts with a dominant nuclear gene from a wild or cultivated species (Amoah and Grun 1988). Haploids extracted from tetraploid cultivars with restorer genes (Iwanaga et al. 1991b) will partially circumvent this male sterility (Ortiz and Peloquin 1993c). The frequency of the restorer gene was calculated as 0.20 in *S. tuberosum* (Iwanaga et al. 1991b).

D. Occurrence and Inheritance of 2*n* Gametes

Gametes with the sporophytic chromosome number are referred to as 2*n* gametes. Some authors called them "numerically unreduced gametes," but this term is avoided here. Normal gametes in any species have the haploid (*n*) number. Thus, 2*n* gametes would be 2*x* in diploids, 4*x* in tetraploids, and 8*x* in octoploids.

Premeiotic, meiotic, and postmeiotic abnormalities during gamete formation are correlated with the production of 2*n* gametes (Veilleux 1985). There are at least six distinct possible modes of 2*n* gamete formation: premeiotic doubling, first division restitution (FDR), chromosome replication during meiotic interphase, second division restitution (SDR), postmeiotic doubling, and apospory where a diploid embryo sac is formed directly from a nucellus or integument cell (Peloquin et al. 1989b). Hermsen (1984) and Peloquin et al. (1989b) discussed in detail the mechanisms and implications of 2*n* gamete formation in crop plants. FDR and SDR mechanisms are the most common modes of 2*n* pollen and 2*n* egg formation in potato. On average, heterozygous diploid parents producing either FDR or SDR 2*n* gametes transmit about 80% and 40%, respectively, of their heterozygosity to the tetraploid offspring.

1. 2*n* Pollen. Parallel orientation of the spindles in the second meiotic division is the most frequent mechanism of 2*n* pollen formation in most tuber-bearing *Solanum* spp. (Masuelli et al. 1992; Watanabe and Peloquin 1993; Oliveira et al. 1995). This meiotic abnormality is under the genetic control of the recessive gene *ps* (parallel spindles), which appears to be ubiquitous among *Solanum* species (Watanabe and Peloquin 1988, 1991; Yerk and Peloquin 1988; Ortiz 1994). However, 2*n* pollen frequency could be affected by variable expressivity and incomplete penetrance. One or two modifier genes appear to be responsible for the variable expressivity of 2*n* pollen production in diploid potato (Ortiz and Peloquin 1992a). Carputo et al. (1995) indicated that minor genes could prevent dyad or triad formation at the end of meiosis despite the occurrence of parallel or tripolar spindle orientation in metaphase II. Also, plant age and environment influence the expressivity of 2*n* pollen. High 2*n* pollen frequency was observed between the second and fifth flowering week (Filotico et al. 1995). Similarly, optimum temperature (Haynes et al. 1987; Cunha et al. 1994) and long photoperiod (Owen et al. 1988) enhance the frequency and viability of 2*n* pollen. Most hybrids with 2*n* pollen production in excess of 10% exhibited stable 2*n* pollen expressivity across environments (Bani-Aameur et al. 1992).

There are conflicting reports about the polygenic control for frequency of 2*n* pollen in diploid populations. For example, the heritability was 0.71 in a *S. phureja-S. chacoense* diploid breeding population (Bani-Aameur et al. 1992), which indicates further gain in 2*n* pollen production by selecting and intercrossing 2*n* pollen producers (or diplandroids). However, diallel analysis of 2*n* pollen frequency revealed that variation between diverse populations derived from intermating diplandroids was due to significantly higher SCA than GCA (Camadro et al. 1992/1993; Qu et al. 1995, 1996). The genotype-by-environment interaction affected the frequency of 2*n* pollen, as shown by the moderate broad-sense heritability. Narrow-sense heritability was low, suggesting that

additive variance was small. Despite these contradictory results, phenotypic recurrent selection was effective for improving the frequency of 2*n* pollen in diploid breeding populations (Ortiz and Peloquin 1992a).

Some haploids and haploid-species hybrids could have FDR and SDR 2*n* pollen formation (Oliveira et al. 1995; Conicella et al. 1996). Incomplete penetrance and variable expressivity of the meiotic mutant alleles controlling 2*n* pollen formation explain this behavior (Ortiz and Peloquin 1992a). However, only one mechanism should be functional in a single pollen mother cell. For example, the occurrence of premature cytokinesis after the first meiotic division precludes the formation of 2*n* pollen by parallel orientation of the spindles in the second meiotic division.

2. 2*n* Eggs. Omission of the second division after a normal first division appears to be the most common mode of SDR 2*n* egg formation in potato haploids, and haploid-species hybrids (Werner and Peloquin 1987; 1991c). This meiotic abnormality is controlled by a recessive meiotic mutant (*os*) in diploid potato (Werner and Peloquin 1990), whose frequency varied between 0.28 and 0.76 in diploid potato species (Ortiz and Peloquin 1991a). Genetic background and environment affect the expressivity of this gene, which also shows incomplete penetrance (Ortiz and Peloquin 1991a). The frequency of modifier genes, which enhance 2*n* egg expressivity, could be increased by recurrent selection with progeny testing (Ortiz and Peloquin 1992a). Some diploids may form 2*n* eggs by a mixture of SDR and FDR mechanisms (Conicella et al. 1991; Werner et al. 1993).

3. Synaptic Mutants Affecting Mega- and Microsporogenesis. Synaptic mutants affecting megasporogenesis and microsporogenesis exist in haploids, species, and haploid-species hybrids in potato (Jongedijk and Ramanna 1988; Parrot and Hanneman 1988; Peloquin et al. 1989b). These meiotic mutants cause either poor pairing or reduced chiasma formation, or both, thereby affecting recombination in meiosis (Jongedijk and Ramanna 1988). A synaptic mutant (sy_3) found in *S. phureja*-haploid hybrids, when combined with parallel spindles, produces FDR 2*n* pollen with no crossing over (FDR-NCO) (Peloquin et al. 1989b). Similarly, a desynaptic gene (*ds-1*) produces completely sterile haploid (*n*) and fertile FDR 2*n* eggs through pseudohomotypic division, i.e., a direct equational division of univalent chromosomes at anaphase I (Jongedijk et al. 1991b). SDR 2*n* gametes from desynaptic mutants are sterile as a result of aneuploidy. This desynaptic mutant substantially reduces chiasma frequency and randomly alters chiasma distribution along individual chromosomes (Jongedijk and Ramanna 1989). Desynaptic gametes may transfer about 95% of the parental diploid genotype intact to the tetraploid offspring.

E. Endosperm Balance Number (EBN), Interspecific Hybridization, and Ploidy Levels

The endosperm balance number in potato and the polar nuclei activation hypothesis in oat (PNA) involve the same concept (Katsiotis et al. 1996). EBN and PNA were developed to interpret, explain, and predict interspecific and interploidy crossability in *Solanum* and *Avena* species, respectively. The EBN originated as an ancient isolating mechanism for keeping diploid fidelity (Ehlenfeldt and Ortiz 1995). Evidence exists for the occurrence of endosperm dosage requirements in other angiosperm genera (Ortiz and Ehlenfeldt 1992). However, complex patterns observed in some crossing outcomes between *Solanum* species could not be explained solely by EBN, which suggested that EBN may be a part of a more complex system of interspecific barrier (Masuelli and Camadro 1997).

1. EBN. The EBN explains endosperm development after intra- and inter-specific crosses. EBN should be in a 2:1 maternal to paternal ratio for normal endosperm development (Johnston et al. 1980). The EBN has been determined for most *Solanum* species by crossing each with standard species of known EBN (Hanneman 1994). Most North and Central American diploid species are 1 EBN, whereas tetraploids are 2 EBN and hexaploids are 4 EBN. For example, all Mexican diploid *Solanum* species, except *S. verrucosum* Schlechtd., are 1 EBN like *S. commersonii* Dun., a diploid species from Argentina (Bamberg and Hanneman 1990). Most South American diploid species are 2 EBN, whereas the polysomic tetraploids are 4 EBN (Hanneman 1994). Thus, species of the same ploidy are isolated from each other by EBN, whereas gene flow may occur between species of different ploidy but similar EBN. Crosses between species with different EBN could be easily made when one of the species produces 2*n* gametes (*see* Section IIIA).

The endosperm balance number appears to be under oligogenic control in potato. Ehlenfeldt and Hanneman (1988) proposed three unlinked additive loci in a threshold-like system to control endosperm development in diploid *Solanum* species. Another genetic model, consisting of two independent loci controlling the EBN with two alleles in homozygosity, was suggested by Camadro and Masuelli (1995). In their system, the EBN in disomic tetraploid *S. acaule* is under the control of two homozygous loci, each with the alleles "1/2" and "0." Similarly, the EBN in diploid *S. gourlayi* Hawkes is controlled by two homozygous loci carrying the allele "1/2," whereas two homozygous loci, each with the alleles "1/2" and "0," control the EBN in diploid *S. commersonii*. Thus, *S. acaule*, *S. commersonii*, and *S. gourlayi* are 2 EBN, 1 EBN, and 2 EBN species, respectively.

2. Ploidy Levels. Crosses between diploid parents with variable expressivity of 2*n* gametes generally produce tetraploid and diploid offspring (Ortiz and Peloquin 1991b). Mitotic chromosome counts (Watanabe and Orrillo 1993) or mean number of chloroplast in stomata may be used to distinguish ploidy after such crosses. Triploids from a 4*x*-2*x* cross (or reciprocal) within the same *Solanum* species are rare due to the endosperm imbalance known as "triploid block" (Marks 1966). The occurrence of this "triploid block" in 4*x*-2*x* or 2*x*-4*x* crosses may be a variable phenomenon, which could explain the rare occurrence of viable triploid offspring from such crosses (De,Maine 1994a). The EBN is a factor enhancing tetraploid hybrid production and suppressing the proportion of seeds with triploid embryos (Johnston et al. 1990; Ortiz and Ehlenfeldt 1992). This endosperm dosage system is typical of species possessing a "triploid block" (Ehlenfeldt and Ortiz 1995). However, triploids from crosses between tetraploids and diploids may arise occasionally from low probability non-heritable random events such as misfertilization, mitotic abnormalities in the gametophyte, and/or mitotic misdivisions in the endosperm (Johnston and Hanneman 1995).

III. GENE INTROGRESSION AND INCORPORATION

The use of haploids for germplasm enhancement at the diploid level, the availability of 2*n* gametes for sexual polyploidization, and the knowledge provided by the EBN for crossing schemes and to predict ploidy, have made a broad spectrum of *Solanum* genetic resources accessible to potato breeders (Peloquin et al. 1989b). There are two approaches for the utilization of exotic germplasm by plant breeders: gene introgression or incorporation (Simmonds 1993). Introgression comprises the transfer to adapted stocks of one or few alleles controlling a desired characteristic, whereas incorporation consists of a large-scale program to develop locally adapted populations to broaden the genetic base of the crop. Both schemes in potato breeding are discussed below.

A. 2*n* Gametes, Bridge Species, Double Pollination, and Embryo Rescue for Utilization of 4*x* (2 EBN) and 2*x* (1 EBN) Species

Crossability barriers between disomic (2 EBN) and tetrasomic (4 EBN) tuber-bearing tetraploid *Solanum* species are broken through double pollination and embryo rescue (Iwanaga et al. 1991a; Singsit and Hanneman 1991a; Watanabe et al. 1995c). A second pollination with 2*n* pollen

from a diploid (2 EBN) species in crosses between tetrasomic (maternal parent) and disomic (paternal parent) tetraploid species reduced premature fruit dropping. Immature embryos can be rescued to circumvent inter-EBN postzygotic barriers by in vitro techniques. Also, hexaploid hybrids (4 EBN) are recovered easily by crossing disomic tetraploid species and *S. tuberosum* (4 EBN), when the disomic tetraploid species produce 2*n* eggs or 2*n* pollen (Brown and Adiwilaga 1990; Camadro and Espinillo 1990; Adiwilaga and Brown 1991). Hexaploid (4 EBN) hybrids could be backcrossed to *S. tuberosum* to obtain pentaploid (4 EBN) offspring (Fig. 2.2). A second backcross of this pentaploid offspring to *S. tuberosum* allows the production of tetraploid (4 EBN) or chromosome addition lines; i.e., 4*x* + extra chromosome(s).

An alternative method was proposed by Bamberg et al. (1994) to introgress genes from disomic tetraploid germplasm using chromosome-doubled *S. commersonii* (4*x*, 2 EBN) as the bridge species. Their derived fertile F_1 hybrids or F_2 offspring producing 2*n* gametes may be crossed with *S. tuberosum* to obtain hexaploid (4 EBN) offspring. With this approach, many hybrids may be produced because the F_1 hybrids are relatively fertile. Also, tetraploid hybrids with *S. commersonii* produce 2*n* gametes, which are needed for crossing with tetraploid *S. tuberosum* and to break restricted recombination within disomic genomes. Last but not least, this approach employs simple crossing techniques and tools.

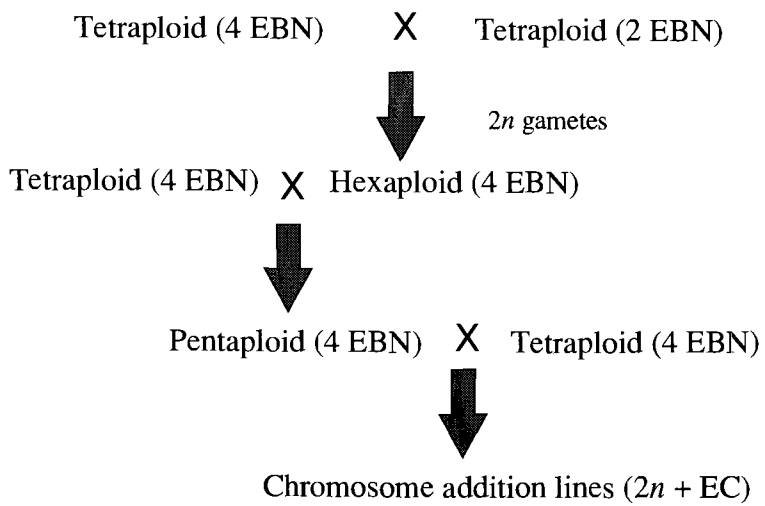

Fig. 2.2. Chromosome engineering for the incorporation of genetic resources of tetraploid (2 EBN) *Solanum* species to the cultivated tetraploid gene pool. EC = extra-chromosome(s).

Interspecific hybridization among diploid *Solanum* species may be affected by stylar barriers (Fritz and Hanneman 1989; Novy and Hanneman 1991). Pollen tube growth could be inhibited in the upper third of the style in interspecific crosses between tuber-bearing species, or just below the stigma in crosses between tuber-bearing and non-tuber bearing species. Reciprocal crosses and EBN manipulation could solve this problem for gene transfer among *Solanum* species. For example, the diploid species *S. chacoense* (2 EBN) and *S. commersonii* (1 EBN) are sympatric species from Argentina. *S. chacoense* possesses stylar barriers that prevent fertilization by *S. commersonii*. However, triploid hybrids could be recovered by crossing *S. commersonni* producing 2*n* eggs and *S. chacoense* with normal *n* pollen (Ortiz and Ehlenfeldt 1992). These triploid hybrids may act as a genetic bridge for gene transfer in potato breeding (Fig. 2.3). Similarly, diploid *Solanum gourlayi* (2 EBN) appears to be another successful bridge species for utilization of *S. commersonii* genetic resources. Triploid hybrids were obtained by crossing *S. commersonii* (producing 2*n* eggs) with *S. gourlayi* (producing *n* pollen). Cytological analysis and fertility of these triploid hybrids indicated that the chromosomes from both species are highly homologous,

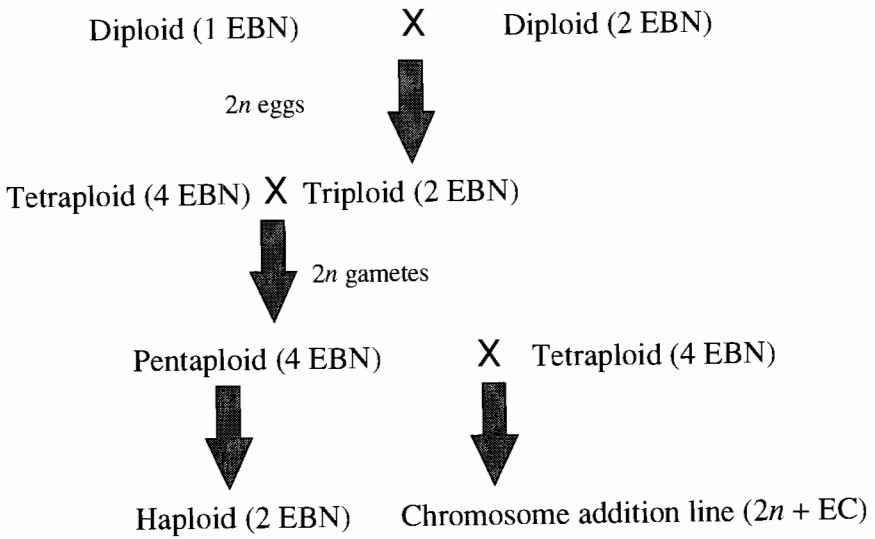

Fig. 2.3. Ploidy manipulation and chromosome engineering for the incorporation of genetic resources of diploid (1 EBN) *Solanum* species to the cultivated tetraploid gene pool and diploid breeding population. Maternal haploids of pentaploid (4 EBN) could be obtained through parthenogenesis. EC = extra-chromosome(s).

allowing gene exchange in meiosis (Masuelli and Camadro 1992). Such triploid hybrids could be crossed with other *Solanum* species to develop diploid (2 EBN) and pentaploid (4 EBN) stocks, or chromosome addition lines (Fig. 2.3). Similarly diploid and triploid hybrids were obtained by crossing a female *S. circaeifolium* Bitt. (2*x*, 1 EBN) with diploid (2 EBN) species, and applying embryo rescue for germination of young seeds (Louwes et al. 1992).

B. Germplasm Enhancement and Population Improvement at the Diploid Level

Germplasm enhancement consists of identifying a useful character in the unadapted *Solanum* germplasm, and transferring appropriate alleles into a usable breeding form by crossing this unadapted (or wild) germplasm with haploids or cultivated species. The end products of this breeding endeavor may be deficient in certain characteristics. Nevertheless, they are still attractive to potato breeders because this improved germplasm has better breeding value than the wild or unadapted original germplasm source of useful allelic variation. For example, selection for tuberization in wild *Solanum* populations unadapted to long daylength was not promising (Jacobsen and Janksy 1989). Hence, *Solanum* species were crossed to haploids of *S. tuberosum* to derive hybrids that tuberized under long daylength.

Haploids from resistant cultivars with genes from wild species offer a promising source of resistance alleles. Haploids resistant to potato viruses or late blight are easily obtained from European and Mexican tetraploid cultivars, respectively (Swiezynkski et al. 1989; Ortiz et al. 1994). Resistant haploids may be crossed with other available sources of resistance in compatible wild species for pyramiding resistance. This scheme has the advantage of combining resistance genes without the need to transfer resistance through the complex methods discussed above (*see* Section IIIA).

The power of germplasm enhancement accelerated the use of wild *Solanum* germplasm for potato breeding in the last decade. Populations with specific resistance to late blight (Swiezynksi et al. 1991), *Erwinia* soft rot (Zimnoch-Guzowska and Lojkowska 1993; Wolters and Collins 1994), potato leaf roll virus (Swiezynksi et al. 1989), potato virus X, potato virus Y (Vallejo et al. 1994c), potato tuber moth (Ortiz et al. 1990), and root-knot nematodes (Iwanaga et al. 1989) were developed through this breeding technique. Also, potato germplasm adapted to short daylength and exhibiting multiple pest and disease resistance was selected using diverse genetic stocks at the International Potato Center

(CIP) in Perú (Ortiz et al. 1994; Watanabe et al. 1995b, 1996b). Other advanced diploid breeding populations of *S. phureja-S. stenotomum* Juz. et Buk. adapted to long daylength were developed through phenotypic recurrent selection at North Carolina State University (Raleigh, USA), and the Scottish Crop Research Institute (Dundee, UK).

Diploid cultivated species have been crossed with diploid wild species for germplasm enhancement at the diploid level. For example, *S. phureja* adapted to long daylength can enhance, as female parent, the breeding value of wild *S. chacoense* (Bani-Aameur et al. 1993). However, the source of cytoplasm appears to be important in germplasm enhancement at the diploid level (Hilali et al. 1988). Cytoplasm of cultivated *S. tuberosum* was superior to the cytoplasm of *S. phureja* for tuber yield, tuber set, and vine maturity. The reverse was true for vine vigor, and time for true seed germination. Hilali et al. (1987) indicated that gamete selection, pseudo-self-incompatibility, and interaction of specific cytoplasm with nuclear genes and the environment could explain this contrasting performance. Also, the specific photoperiodic requirements for tuberization of the maternal parents may account for the divergent reciprocal phenotypes. Conversely, chromosomally encoded genes, resulting from maternal or paternal effects, explained distinct tuber characteristics in reciprocal backcrosses (Amoah et al. 1988).

Enlarged pollen size has been the major indicator for the occurrence of $2n$ pollen. Normally, $2n$ pollen is 1.25 times as long as n pollen. Diploids with a high frequency of $2n$ pollen are selected to pollinate tetraploids to obtain a high frequency of tetraploids offspring through sexual polyploidization. Also, separation of $2n$ pollen from a heterogeneous mixture may be achieved by velocity sedimentation (Simon and Sanford 1990). With this system, only viable $2n$ pollen will be available for crosses with diploid $2n$ egg producers (diplogynoids) or tetraploid cultivars. The number of seeds per fruit after $2x$-$4x$ crosses provides an estimate of $2n$ egg frequency in diploid potato. This screening method has been the most popular to select diplogynoids in breeding populations (Ortiz and Peloquin 1991a; Barone et al. 1993).

Diploid hybrids producing $2n$ gametes and with the desired characteristic(s) are selected for further production of tetraploid hybrids via unilateral ($4x$-$2x$ or $2x$-$4x$ crosses) or bilateral ($2x$-$2x$ crosses) sexual polyploidization. Early vigor, profuse early flowering, and occasionally late maturity have been associated with $2n$ pollen production (Yerk and Peloquin 1989a). Hence, simultaneous selection for earliness and $2n$ pollen production may be required in some diploid populations.

Sometimes, resistance from wild species may be associated with poor agronomic characteristics such as late maturity (Swiezynski et al. 1991). Therefore, germplasm enhancement will be required to improve

the agronomic performance of the diploid breeding population, at the same time retaining the desired introgressed alleles such as resistance genes. However, such associations between late maturity and resistance may exist in tetraploid cultivars (Swiezynski 1990). This finding suggests a common pleiotropic physiological control rather than a genetic correlation due to linkage. Consequently, it may be difficult to overcome this association through sexual recombination.

In advanced breeding populations, tuber quality may be associated with specific disease resistance. For example, high starch content in tubers correlated with resistance to *Erwinia* soft rot in diploid potato (Zimnoch-Guzowska and Lojkowska 1993). Furthermore, selection for tuber characteristics such as smoothness, shape, and size maintained high specific gravity in a diploid breeding population (Haynes and Haynes 1990).

Diploid germplasm is a valuable source of desired resistance alleles for potato breeding. Diploids with multiple resistance to pests and diseases were released by CIP in the early 1990s (Watanabe et al. 1994a). Also, the diploid DW 84-1457 was released by the Mlochow Centre of the Institute for Potato Research in Poland (Dziewonska and Was 1994). This diploid stock possesses highly heritable non-hypersensitive resistance to infection and multiplication of potato leaf roll virus, extreme resistance to potato virus X, high resistance to potato virus M, and good table and processing tuber quality. DW 84-1457 has been a parent of diploid and tetraploid breeding populations in Poland. This diploid and CIP germplasm are available for international exchange.

The potential of diploid hybrids for cultivar development was tested in some breeding populations (Watanabe et al. 1996a). Some diploid hybrids developed at CIP outyielded tetraploid cultivars (Watanabe et al. 1996b). This germplasm may fulfill the demand of local ethnic markets accustomed to diploid potatoes, e.g., in the Andean region of South America.

C. Transfer of Resistance from Wild Species to the Tetraploid Breeding Pool

Chemical protection may control pests and diseases on susceptible potato cultivars. However, host plant resistance offers other advantages for pest and disease control in sustainable, environmentally friendly agricultural systems. For example, nematode density appears to be greater in nematicide-treated plots of susceptible cultivars than on untreated plots of partially resistant cultivars (Gurr 1987). This result shows the advantage of host plant resistance for control of this pest as compared to chemical pesticides. Furthermore, for some diseases

(e.g., *Erwinia* soft rot) cultural practices or pathogen-free tubers are ineffective at reducing yield losses (Zimnoch-Guzowska and Lojkowska 1993). Hence, host plant resistance offers the best control option.

1. Chromosome Engineering. Genetic resources from hexaploid (4 EBN) species are easily transferred to the cultivated gene pool through direct hybridization with tetraploid (4 EBN) cultivars. For example, many cultivars possess genes for late blight resistance from *S. demissum* (Ross 1986; Plaisted and Hoopes 1989). Also, resistance genes for Columbia root-knot nematode (*M. chitwoodi* Golden, O'Bannon, Santo & Finley) races 1 and 2 were transferred from *S. hougasii* Corr. to the cultivated gene pool following this approach (Brown et al. 1991).

Resistance to potato leaf roll virus was transferred from the non-tuber bearing diploid (1 EBN) *S. etuberosum* Lindl. to tuberous potato germplasm using interspecific sesquiploidy (Chavez et al. 1988a). This research was an important step to introgress alien genes from genomes that share little homology. This scheme (Fig. 2.4) consists of the construction of hybrids possessing the sporophytic chromosome number of

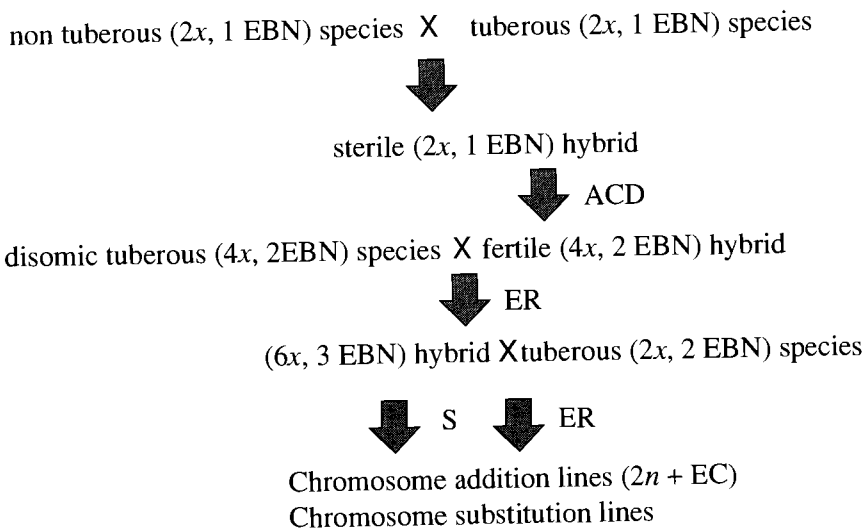

Fig. 2.4. Sesquiploidy and development of chromosome addition or substitution lines to transfer desired alleles to a tuber-bearing *Solanum* breeding pool from a non-tuber bearing *Solanum* species. Postzygotic EBN barriers are circumvented by embryo rescue. ACD = asexual chromosome doubling, ER = rescue of immature embryos, S = selfing, EC = extra-chromosome(s).

one species and the haploid set of another species from which desired alleles are extracted. Embryo rescue circumvents the EBN postzygotic barriers after interspecific hybridization of species with unequal EBNs. This procedure shows the role of 2*n* gametes to produce sesquiploids harboring non-homologous genomes bearing desired alleles. The sporophytic complement is transferred through 2*n* gametes, while the desired allele is transmitted by a parent producing *n* gametes (Chavez et al. 1988b). Balance partitioning, during meiosis of the chromosomes from the parent with the sporophytic complement, buffers the unequal distribution of chromosomes from the other species even after abnormal chromosome pairing. Tuberous chromosome addition and substitution lines bearing the desired allele from the non-tuber bearing *Solanum* species may be obtained through this procedure.

Extreme resistance to potato virus Y (strain PVY^0) was transferred from the non-tuberous diploid (1 EBN) *Solanum brevidens* Phil. to tuber-bearing diploid hybrids (Valkonen et al. 1995). The interspecific diploid hybrids were produced by direct crossing between *S. brevidens* and a diploid (2 EBN) hybrid followed by rescue pollination with diploid *S. phureja* IvP-35. This rescue pollination promoted fruit development, and immature embryos were rescued by in vitro techniques to circumvent postzygotic EBN barriers. All the interspecific diploid hybrids were susceptible to potato virus A and potato leaf roll, although *S. brevidens* showed extreme resistance to both viruses. Surprisingly, two interspecific diploid hybrids reacted with hypersensitivity to potato virus X. This plant host response to potato virus X was observed in IvP-35 but not in *S. brevidens* or the other diploid parent. This observation suggested an intergenomic translocation (Wilkinson et al. 1995) of a small chromosome segment bearing the hypersensitivity gene from IvP-35. Such chromosomal aberration may occur during zygote and embryo development after distant hybridization between *Solanum* species. Hence, this phenomenon offers an alternative path to introgress specific chromosome segments bearing useful characteristics from some *S. phureja* to other diploid potato breeding pools.

Solanum acaule possesses extreme resistance to potato spindle tuber viroid. Watanabe et al. (1992a) compared four methods for gene introgression from this disomic tetraploid (2 EBN) species to the cultivated tetraploid (4 EBN) gene pool. Three methods consisted of bridge crossing with a compatible diploid (2 EBN) species to obtain either triploid hybrids for crossing with a tetraploid cultivar, or triploid non-2*n* pollen-producing hybrids for further asexual polyploidization with colchicine or through micropropagation (Sonnino et al. 1988). The fourth method combined direct hybridization between a tetraploid cultivar and

S. acaule with a second compatible pollination. Immature embryos from such crosses were excised for in vitro germination (i.e., embryo rescue). The latter was recommended by Watanabe et al. (1992a) as the most efficient method for the utilization of genetic resources from *S. acaule*. Moreover, the F_1 hybrids between *S. tuberosum* and *S. acaule* had tuber yield and appearance similar to that exhibited by the cultivated tetraploid species (Watanabe et al. 1994b), which showed the potential of this approach for germplasm enhancement of the potato genome.

2. Sexual Polyploidization. The advantages of sexual polyploidization for transfer of monogenic and polygenic resistance from the diploid level to the tetraploid level were summarized by Ortiz and Peloquin (1993c). Resistance genes from wild species to control bacterial wilt (Watanabe et al. 1992b; Charkbararti et al. 1994; Ortiz et al. 1994), common scab *Streptomyces scabies* (Thaxter) Waksman & Henrici (Murphy et al. 1995), cyst nematodes (Ortiz et al. 1997a), early blight *Alternaria solani* Sorauer (Herriot et al. 1990), potato tuber moth (Watanabe et al. 1995b), and root-knot nematodes (Iwanaga et al. 1989) were successfully transferred to the cultivated gene pool using FDR 2*n* pollen. Also, resistance to infestation by potato leafhopper (*Empoasca fabae* Harris) in 4*x*-2*x* hybrids derived from direct crossing with *S. chacoense* was greater than, but severity of leaf necrosis was equal to, that exhibited by the susceptible tetraploid check cultivar (Sanford and Ladd 1992). However, De,Maine et al. (1993a) reported that resistance to common scab, potato leaf roll virus, and potato virus Y was lower in tetraploid hybrids than in their *S. phureja* progenitor.

Plaisted et al. (1992) released NYL 235-4, a tetraploid hybrid with resistance to Colorado potato beetle [*Leptinotarsa decemlineata* (Say)] and leafhopper. The original source of resistance alleles was *S. berthaultii* Hawkes. The development of NYL 235-4 consisted of a 4*x*-2*x* cross, followed by six generations of sexual recombination at the tetraploid level through bulk pollination, backcrossing, and sibmating. The insect resistance was associated to type A glandular trichomes on the abaxial surface of the foliage. The tubers of this hybrid had medium (but still acceptable) glykoalkaloid content (10–11 mg /100 g fresh wt).

D. Assessing the Agronomic Performance and Tuber Quality of Tetraploids from Sexual Polyploidization and Breeding Value of Diploid Parents

Large and significant high- and mid-parent heterosis for tuber yield were reported in potato hybrids derived from 4*x*-2*x* and 2*x*-2*x* crosses (Birhman and Garg 1989; Darmo and Peloquin 1991; Werner and Peloquin 1991b; Peloquin and Ortiz 1992; Ortiz and Peloquin 1993a). The breeding value of diploid hybrids from diverse wild species was also determined in the last decade (Yerk and Peloquin 1990a; Darmo and Peloquin 1991; Ortiz et al. 1997b). The tetraploid cultivar 'Krantz', a russet cultivar adapted to irrigated sands in the U.S. North-Central region, was developed using ploidy manipulations (Lauer et al. 1988).

1. Agronomic Traits, Adaptation, and Yield Stability. Tetraploid offspring from 4*x*-2*x* crosses outyielded their half-sibs 4*x*-4*x* or tetraploid cultivars when the diploid parent produces FDR 2*n* pollen (Darmo and Peloquin 1991; Ortiz et al. 1991b, 1997b). Heterosis for tuber yield may result from the multiplicative interaction between tuber number and average tuber weight (Carroll and De,Maine 1989).

Selected 4*x*-2*x* hybrids showed stable higher yield than tetraploid cultivars across environments in long and short daylength, respectively (Darmo and Peloquin 1990; Ortiz et al. 1997b). However, locally adapted tetraploid female parents are required for the success of this breeding approach (Yerk and Peloquin 1990a; Ortiz et al. 1991a). Also, the target environment may allow the expression of favorable traits from alien germplasm to obtain high yielding tetraploid hybrids (Bani-Aameur et al. 1991).

Tetraploid hybrids from FDR diplandroids had higher yield, tuber set, and tuber weight than their reciprocal tetraploids derived from SDR diplogynoids (Hutten et al. 1994a). FDR and SDR derived offspring showed similar vine maturity and chip color. Furthermore, vine maturity of derived offspring from 4*x*-2*x* crosses was predicted by the parental performance (Hutten et al. 1996). However, there was a low parent-offspring correlation for total yield and yield components (De Jong and Tai 1991; Keijzer-van der Stoel et al. 1991). These results confirmed that tuber yield and components are maximized by non-additive intra- and interlocus interactions, while vine maturity was highly heritable.

The breeding values of haploid-species hybrids producing FDR 2*n* pollen and their derived vegetatively doubled (CD2*x*) counterparts were analyzed in their tetraploid hybrid offspring (Tai and De Jong 1997). The 4*x*-2*x* hybrids outperformed the 4*x*-CD2*x* for total and marketable tuber yield. The variance for tuber appearance, eye depth, specific gravity, and tuber size was smaller in the tetraploid offspring from FDR diplandroids than that observed in the hybrid offspring from CD2*x*. The results suggested that genes for these tuber characteristics are close to the centromere in respective chromosomes. Although some heterotic loci for high yield were close to the centromere (Tai and De Jong 1997), a similar analysis

suggested that most genes for tuber yield would be scattered between the centromere and the site of maximum recombination.

Diploid parents differed significantly in their general combining ability for tuber yield and components in 4*x*-2*x* and 2*x*-2*x* crosses (Ortiz et al. 1988; Keijzer-van der Stoel et al. 1991; Tai and De Jong 1991; Clulow et al. 1995), which reinforces the idea that selection of elite diploid progenitors for a regular breeding program must be based on progeny testing. Factorial mating designs with common tetraploid testers have been the most frequent method to assess the breeding value of diploid parents. The tester(s) should be unrelated to the parents to be tested and should have a low frequency of favorable alleles so that the differences in the breeding value among parents can be manifested.

Selected tetraploid hybrids derived from bilateral sexual polyploidization had higher yield and dry matter content than tetraploid check cultivars (Werner and Peloquin 1991b; Ortiz and Peloquin 1993a; Rouselle-Bourgeois and Rouselle 1995). Tetraploids always outyielded their sib diploids from the same 2*x*-2*x* crosses (Peloquin and Ortiz, 1992; Hutten et al. 1995a). Diploid hybrids had smaller tubers but similar vine maturity than their tetraploid full-sibs. Werner and Peloquin (1991b) recommended the development of diploid elite progenitors with high frequency of 2*n* gametes and desired tuber characteristics for regular production of tetraploid cultivars. Routine production of tetraploid hybrids may be achieved by crossing FDR diploid parents when the female parent produces megaspores through pseudohomotypic division due to a desynaptic mutant (Jongedijk et al. 1991b).

2. Tuber Quality. Tetraploid hybrids from 4*x*-2*x* crosses showed higher specific gravity and better general tuber appearance than those derived from 4*x*-4*x* crosses (Darmo and Peloquin 1991). Selected 4*x*-2*x* hybrids had higher or similar specific gravity and chip-processing ability than processing cultivars (Peloquin and Ortiz 1992). The diploid parents of these hybrids produced FDR 2*n* pollen by parallel spindles, and had *S. tarijense* (Hawkes) in their pedigree.

Chip color was the same but specific gravity was higher in tetraploid offspring derived from FDR parents than in those derived from SDR parents (Hutten et al. 1996). Based on the diploid parental performance, specific gravity was predicted in the tetraploid offspring derived from 4*x*-2*x* or 2*x*-2*x* crosses (Keijzer-van der Stoel et al. 1991). The ranking of general combining ability (GCA) of the diploid parents was the same in either mating scheme. These results suggested that the best diploid parents for specific gravity could be selected after progeny testing at the diploid level.

S. phureja had tubers with high culinary quality; however, its F_1 hybrids with *S. tuberosum* showed poor culinary quality (De,Maine et al. 1993b). The backcross breeding method may improve the culinary quality. Nevertheless, a tetraploid hybrid derived from *S. phureja* was released in Canada as the cultivar 'Yukon Gold' in the early 1980s (Johnston and Rowberry 1981). This medium-early cultivar, with yellow tuber, was selected due to its high quality as table potato and for French fry processing.

IV. GENETIC ANALYSIS WITH SPECIES, HAPLOID-SPECIES HYBRIDS, AND 2*N* GAMETES

Genetic analysis at the diploid level has much greater resolution than at the tetraploid level due to disomic inheritance. Therefore, potato geneticists prefer to investigate the potato genome with haploids, diploid species, or diploid hybrids between haploids and other *Solanum* species. Non-inbred heterozygous parents are mostly used because monofactorial gametophytic self-incompatibility (Trognitz and Schmiediche 1993) and severe inbreeding depression prevent the development of diploid inbred lines in potato. Double monoploids had lower female fertility compared to the anther donor but they produced sufficient seed to facilitate their utilization in a breeding program (M'Ribut and Veilleux 1992). However, they were considered to be male sterile for practical purposes.

The use of 24-chromosome potatoes for genetic analysis until the early 1990s was recently reviewed by Ortiz and Peloquin (1994b). In addition to this approach for genetic analysis of the potato, tetraploid-diploid crosses provide a means for gene-centromere mapping (Mendiburu and Peloquin 1979). Map distances are measured by the frequency of nulliplex (recessive) genotypes in the tetraploid offspring. Tetraploid hybrids are derived by crossing a nulliplex tetraploid with a heterozygous diplandroid. Half-tetrad analysis determines accurately the position of the centromere in relation to other loci in respective chromosomes, especially in saturated molecular maps of potato. Tai (1994) has discussed extensively the use of 2*n* gametes in potato genetics until the early 1990s.

A. Diploid Level

Monogenic, oligogenic, and polygenic systems control most important characteristics in potato (Table 2.3). Resistance to most diseases and some insect pests are highly heritable, which makes easy gene transfer

Table 2.3. Conventional Mendelian and quantitative genetic analysis in 24 chromosome potato.

Characteristics	Population	Gene Action or Heritability (h^2)	Reference
Resistance			
Early blight	Wild-cultivated hybrids	Additivity ($h^2 = 0.64-0.78$)	Ortiz et al. 1993c
Late blight	*S. phureja*	Moderate resistance due to minor genes	Canizares and Forbes 1995
	Haploids of Mexican resistant cultivars	Additive effects are more important in determining the level of field resistance	cited by Ortiz et al. 1994
	Wild-cultivated hybrids	Major and minor modifier resistance genes in resistant and susceptible parents	Colon et al. 1995b; El-Kharbotly et al. 1996b
		General combining ability effects of major genes predominant, but small specific combining ability in *S. microdontum*. Dominant gene action in some crosses	Swiezynksi et al. 1991
Verticillium wilt	Wild species	Complex polygenic inheritance	Concibido et al. 1994
Bacterial wilt	*S. sparsipilum*	Polygenic and affected by temperature	cited by Ortiz et al. 1994
Soft rot	*S. phureja - S. stenotomum*	Significant genetic variation, although low to medium heritability	Wolters and Collins 1995
PLRV	*S. chacoense*	Simple dominant gene	Brown and Thomas 1994
	Diploid breeding population	Cumulative effect of dominant genes	Swiezynski et al. 1993
PVX	*S. phureja - S. stenotomum*	Dominance of two genes controlling resistance to U.S. common strain	Vallejo et al. 1995
	Haploids with resistance from *S. stoloniferum*	One single dominant gene for immunity	Ortiz et al. 1994
PVY	*S. phureja - S. stenotomum*	Complementary action of two dominant genes controlling resistance to PVY^0	Vallejo et al. 1995
	Haploids from *S. andigena*	Immunity (Ry_{Adg})and hypersensitivity (Ny) are controlled by non-allelic independent genes	Ortiz et al. 1994
	Haploids with resistance from *S. stoloniferum*	One single dominant gene for immunity (Ry_{sto})	Ortiz et al. 1994
	Diploid hybrids	Immunity is epistatic to hypersensitivity to PVY^0	Valkonen et al. 1994
Potato tuber moth	Wild-cultivated hybrids	Simple inheritance due to additivity; resistant cytoplasm not essential	Ortiz et al. 1990
Root-knot nematode	Wild-cultivated hybrids	$h^2 = 0.48-0.62$ in *S. sparsipilum*	Ortiz et al. 1994
Cyst nematode	Wild species	One or two dominant major genes but interacting with minor modifier genes	Dellaert et al. 1988
Golden nematode	Haploids of European cvs.	Dominant genes for Ro_1	Hutten et al. 1995b
Freezing	Wild species and wild-cultivated hybrids	Polygenic partially recessive control of two different components: hardening ability and freezing survival of non acclimated status	Stone et al. 1993; Tucci et al. 1996
Polyphenol oxidase activity	*S. berthaultii*	Co-dominance gene action could explain low h^2	Kowalski et al. 1990
	Wild-cultivated hybrids	(0.08) in defense against insect	Vallejo et al. 1994a,b
Type A and B trichome density	Wild-cultivated hybrids	A: ($h^2 = 0.15-0.59$); B: ($h^2 = 0.00-0.41$)	Vallejo et al. 1994a,b
Crumpled mutant	Wild-cultivated hybrids	Monogenic single recessive gene	Jongedijk et al. 1990
Lethal yellow cotyledon	*S. chacoense*	Two independent recessive epistatic genes	Birhman et al. 1994
	Wild-cultivated hybrids	Monogenic single recessive gene	Jongedijk et al. 1990
Male sterility	Wild-cultivated hybrids	Dominant gene interacting with sensitive cytoplasm; dominant restorer	Ortiz and Peloquin 1993c
Granule bound starch synthetase mutant	Haploids	Monogenic recessive genotype (*amf/amf*) prevents production of amylose in potato starch	Jacobsen et al. 1989
Anthocyanin pigmentation	Review	One locus (*D*) for basic pigmentation; *P* and *R* loci responsible for purple and red pigments. Locus *Ac* controls acylation anthocyanins. Gene *F* acts as intensifier of pigmentation in the flowers and requires *D* and *R* (or *P*) for expression	De Jong 1991
Plant shape	Wild-cultivated hybrids	Variable h^2 (0.00–0.85)	Ortiz and Peloquin 1993a
Vine earliness	Wild-cultivated hybrids	Low h^2 (0.08–0.20)	Ortiz and Peloquin 1993a
Flowering	Wild-cultivated hybrids	Moderate to high h^2 (0.58–0.87)	Ortiz and Peloquin 1993a
Tuber			
Formation under long days	Wild-cultivated hybrids	Moderate to high h^2 (0.52–0.72)	Ortiz and Peloquin 1993a
Ca concentration	*S. phureja - S. stenotomum*	Genetic variation among parents	Wolters and Collins 1995
Size	*S. phureja - S. stenotomum*	Nil h^2 (–0.03)	Wolters and Collins 1995
Eye depth	*S. phureja - S. stenotomum*	Moderate h^2 (0.52)	Wolters and Collins 1995
Shape	*S. phureja - S. stenotomum*	Round gene (*Ro*) dominant over long, and linked (11.8 cM) to *I* (anthocyanin in tuber skin). Gene action explain low h^2 (0.06)	De Jong and Burns 1993 Eck et al. 1994b Wolters and Collins 1995

Table 2.3. *Continued*

Characteristics	Population	Gene Action or Heritability (h^2)	Reference
Skin color	*S. phureja - S. stenotomum*	Moderate h^2 (0.51)	Wolters and Collins 1995
Orange flesh	*S. phureja - S. stenotomum*	*Or* allele (orange) dominant over *Y* allele (yellow) and *y* allele (white) in *Y* locus	Brown et al. 1993 Jongedijk et al. 1990
Flesh pigmentation	*S. phureja - S. stenotomum*	One gene (*Pf*) controls distribution of anthocyanin to the tuber flesh but only in *I* background. *I* controls the pigmentation in tuber skin and seems to be closely linked to *Pf*	De Jong 1987
Processing	Wild-cultivated hybrids	Separate genetic mechanisms control tuber weight and number, specific gravity, and chip color at harvest, after storage at 4°C, and after one week of reconditioning	Serquen and Peloquin 1996
Specific gravity	*S. phureja - S. stenotomum*	Significant genetic variation, affected by genotype-by-year interaction, which explains moderate broad-sense h^2 (0.66)	Haynes et al. 1995; Wolters and Collins 1995
(under high temperature)	*S. phureja - S. stenotomum*	Average narrow-sense $h^2 = 0.28$ (0.07–0.77)	Haynes et al. 1989
Reducing sugar content	Improved diploid population	Depend on genotype and temperature	Jakuczun et al. 1995
Chip color	Wild-cultivated hybrids	Dominant alleles at three loci required for good crisp production (associated to reversion and recondition)	Thill and Peloquin 1994
Tissue culture			
Androgenic competence	*S. phureja*	Simple partially dominant gene. Genes for embryo regeneration act only in the presence of this androgenic gene.	Singsit and Veilleux 1989; Taylor and Veilleux 1992
	Wild-cultivated hybrids	Polygenic complementary recessive gene(s) for embryo formation	Sonnino et al. 1989
Leaf disc regeneration	*S. phureja*	Two recessive independent genes	Taylor and Veilleux 1992
Protoplast culturability	*S. phureja*	Two complementary dominant alleles required for division to occur after protoplast isolation	Cheng and Veilleux 1991; Taylor and Veilleux 1992

or population improvement for biotic stresses in potato breeding. Phenotypic recurrent selection is recommended for characteristics with high heritability. Conversely, insect resistance associated with trichomes in potato has a low medium to low heritability. Most tuber characteristics except size and weight have medium to high heritability. Improvement for polygenic characteristics with low heritability could be achieved by family selection and progeny testing.

B. 2*n* Gametes

Genetic analysis using 2*n* gametes clarified the system controlling genetic-cytoplasmic male sterility in potato (Iwanaga et al. 1991b; Ortiz et al. 1993a). A dominant male sterility gene interacting with a sensitive cytoplasm causes male sterility in potato. Variation for male sterility in 4*x*-2*x* full-sibs was explained by the segregation of a dominant allele restoring male fertility. Male fertility of tetraploid hybrids from sexual polyploidization provides means for their utilization in broadening the genetic base of tetraploid potato breeding populations (Abdul-Baki and Haynes 1993).

Genes for resistance to potato cyst nematode, potato virus X, potato virus Y (Wagenvoort and Zimnoch-Guzowska 1992), genetic-cytoplasmic male sterility (Iwanaga et al. 1991b; Ortiz et al. 1993b), and isozymes (Douches and Quiros 1987) were mapped to respective centromeres by half-tetrad analysis. Segregation from families obtained by two or more 4*x*-2*x* crosses were pooled together for gene mapping when they were homogeneous (Jogendijk et al. 1991a). Ortiz and Peloquin (1993b) mapped the flower pigmentation locus (*F*) using a weighted least-squared procedure (Tai 1994) after pooling data from several crosses.

Theoretical models, sometimes validated by experimental results, were developed to determine the significance of allelic diversity and 2*n* gametes for approaching heterozygosity in tetraploid potatoes (Werner and Peloquin 1991a), to describe the genetic value of tetraploid-diploid hybrids (David et al. 1995), to establish associations between genetic markers with quantitative traits (Ortiz and Peloquin 1992b), and to do marker-based analysis of tetrasomic inheritance of quantitative traits (Tai 1994). A computer simulation was used to compare the genetic consequences of sexual and asexual polyploidization in potato (Watanabe et al. 1991). The covariance between diploid parent-tetraploid offspring was derived for non-inbred parents by computing the coefficient of coancestry and double coancestry (Haynes 1990). The covariance between a haploid-species hybrid and its derived tetraploid hybrid offspring when the same Tuberosum parent was used for haploid extraction

and sexual polyploidization was investigated by Haynes (1992b). She determined that this covariance depends on the mechanism of 2*n* gamete formation and the frequency of single exchange tetrads, and it is a function of the ploidy levels involved. A theoretical investigation suggested large preferential pairing between homologous chromosomes in hybrids derived from interspecific unilateral sexual polyploidization (Haynes et al. 1991). These models may be important tools for gaining insight into the potato genome.

Inbreeding of tetraploid hybrids arising from sexual polyploidization depends on the coancestry and inbreeding of the parents, the coefficient of double reduction for specific loci in the tetraploid parent, and the frequency of single exchange tetrad (β) in the diploid parent (Haynes 1992a). The mechanism of 2*n* gamete production determines β value, which ranges from 0 to 1 for both FDR and SDR (Tai 1994). For chromosomal segregation $\alpha = \beta = 0$, for chromatid segregation $\alpha = 1/7$ and $\beta = 2/3$, and for maximal equational segregation $\alpha = 1/6$ and $\beta = 1$. FDR gametes are more heterozygous than SDR gametes when β is smaller than 2/3. For example, tetraploid hybrids derived by intermating FDR diploid parents are more heterozygous than those obtained by crossing FDR and SDR diploid parents when β is smaller than 2/3 (Haynes and Potts 1993). Similarly, FDR × SDR tetraploid hybrids show lower inbreeding than those derived from SDR × SDR crosses on loci with chromatid segregation.

C. Biochemical and DNA Marker Maps and Molecular Genetic Analysis

Diploid potatoes made possible the extensive genetic mapping within the last decade (Table 2.4), thereby helping to fill the genetic knowledge gap on the potato genome. The total markers mapped on the potato genome (> 1400) make this species among the most thoroughly mapped of the plant and animal kingdoms (Tanksley et al. 1992). Furthermore, genetic maps may assist in the marker-assisted incorporation or introgression of *Solanum* genetic resources into the tetraploid breeding populations. Molecular-aided genetic analysis allowed the dissection of complex quantitative characteristics into their discrete genetic factors (Table 2.5). Also, genetic analysis with molecular markers confirmed early hypotheses about transmission of heterozygosity through 2*n* gametes, and helped to elucidate the mode of 2*n* gamete formation in diploid parents (Table 2.6).

1. Marker-aided Genetic Analysis. New isoenzymatic loci were found in the potato genome using diploid hybrids (Douches and Quiros 1988a).

Table 2.4. Potato genetic maps developed with diploid populations.

Institution	Markers	Population	Features	References
Cornell Univ.	RFLP, isozymes	haploid-species	135 markers with a total genome coverage of 670 cM[z]	Bonerbiale et al. 1988
	RFLP, isozymes	haploid-species	1030 markers with a total genome coverage of 684 cM (ca. 1 marker every 0.7 cM)	Tanksley et al. 1992
Max Plank Inst.	RFLP	haploids	141 markers with a total genome coverage of 690 cM	Gebhardt et al. 1989
	RFLP	haploid	299 DNA markers plus one morphological marker (384 loci) with a total genome coverage of 1050 cM (80–90% of potato genome)	Gebhardt 1994
Université de Montreal (Canada)	RFLP	species	84 markers with a total genome coverage ranging from 206 cM (male map) to 375 cM (female map)	Rivard et al. 1996
Center for Plant Breeding & Reproduction Research and Wageningen Agric. Univ.	RFLP, isozymes, transposons	haploid-species	175 molecular, 10 morphological and 8 isozyme markers with a total genome coverage of 1120 cM	Jacobs et al. 1995
Wageningen Agric. Univ. and Key gene N.V.	RFLP, isozymes, AFLPs	haploid-species	264 AFLPs, 175 molecular, 10 morphological and 8 isozyme markers with a total genome coverage of 1170 cM	Eck et al. 1995
Cornell Univ.– Max Plank Inst.	RFLP	haploid-species	230 DNA markers and 1 morphological marker (304 loci) a total genome coverage of 1034 cM	Gebhardt et al. 1991
Univ. California, Davis	RAPD	species	18 loci segregated, 8 in 3 linkage groups	Quiros et al. 1993
Michigan State Univ.	RAPD, RFLP, isozymes	haploid-species	63 RAPDs, 44 RFLPs, 10 isozymes and 1 morphological marker	Freyre et al. 1994

[z]A genetic distance of 1 cM corresponds to a physical distance of 1 Mb in the potato genome (Ballrova et al. 1995).

Table 2.5. Gene mapping and genetic analysis with biochemical and molecular markers.

Characteristic	Marker System	Population[z]	Chromosome(s)-arm	Phenotypic Variation Explained by Markers	Reference
Resistance					
Late blight					
R_1	RFLP	h-s	5		El-Kharboly et al. 1994
	RFLP	h-s	5S		Leonard-Schippers et al. 1992
	RFLP, AFLP	h-s	2 RFLP tightly linked to R_1 locus in 5S		Meksem et al. 1995
R_3	RFLP	h-s	11-distal position		El-Kharboly et al. 1994
R_6	RFLP	h-s	11-distal position		El-Kharboly et al. 1996a
R_7	RFLP	h-s	11-distal position		El-Kharboly et al. 1996a
Race specific resistance	RFLP	h-s	Extra genetic factors involved in the expression of R_1, R_4, and R_{10} alleles		El-Kharboly et al. 1996b
quantitative	RFLP	h-s	2, 3, 4, 5S (2), 6, 7, 9, 11, 12 (2)		Leonard-Schippers et al. 1994
PVX (extreme)	RFLP	h-s	5S, 12S		Ritter et al. 1991
PVY (extreme,					
Ry_{Adg})	RFLP	h-2x	11 (proximal end)		Hamalainen et al. 1997
(Ry_{sto})	AFLP	4x	11 (proximal end)		Brignetti et al. 1997
Insects (trichomes)	RFLP	h-s			Bonierbale et al. 1994
Type-A trichome density			6, 10 In BC^y: 2, 4	Each 27–40%, both 58%	
Enzymatic browning assay for PPO			6 (large effect), 10	Each 20–52%, both 63%	
PPO concentration			2, 5, 8	Each 11–23%	
Type-B trichome density			5S, 11 In BC^y: 2, 9	Each 9–35%, both 38%	
Sucrose droplet formation			5S	Single recessive gene	
Sucrose ester levels			1S, 2 (2), 4, 5s	Each 6–25%, all 68%	
Oviposition			1, 5, 8, 10	Each 5–12%	
Insect feeding			2, 4, 5, 8	Each 5–13%	
Colorado potato beetle	RFLP	h-s			Yencho et al. 1996
Oviposition			1, 5, 10	Each 4–8%, all 20%	
Insect feeding			5, 10	Each 6–11%, both 25%	
Field defoliation			1, 5, 8	Each 4–6%, both 21–27%	
Cyst nematode (H_1)	RFLP	h-s	5-distal position		Gebhardt et al. 1993
	RFLP	h	5		Pineda et al. 1992
	RFLP^{h-s}		Major gene in 5, and minor genes in 4 and 7		Kreike et al. 1994
Golden nematode (*Gro*)	RFLP	h-s	7 (*S. vernei*)		Gebhardt et al. 1993
	RFLP, RAPD, SCAR	h	Gro_6: 5 (*S. vernei*) linked to H_1		Jacobs et al. 1996
	RFLP	h-s	Gro_1: 9 (*S. spegazzinii*)		Barone et al. 1990
	RFLP	h-s	$Gro_{1.2}$: 10, $Gro_{1.3}$: 11	Both 14%	Kreike et al. 1993
	RFLP	h-s	$Gro_{1.2}$: 10, $Gro_{1.4}$: 3		Kreike et al. 1996
	RFLP, RAPD, AFLP		3 RFLP and 1 RAPD tightly linked in 7		Ballvora et al. 1995
Columbia root-knot nematode	RFLP		Resistance gene at the end of chromosome 11		Brown et al. 1996
Parallel orientation of spindles	Isozymes	h	8		Ortiz et al. 1993a
Desynapsis	RFLP, isozymes	h-s	8		Jacobs et al. 1995

(*continued*)

Table 2.5. *Continued*

Characteristic	Marker System	Population[z]	Chromosome(s)-arm	Phenotypic Variation Explained by Markers	Reference
Self-incompatibility locus	RFLP[s]	s	1		Rivard et al. 1996
	RFLP	h, h-s	1		Gebhardt et al. 1991
Waxiness	RFLP	h	7		Gebhardt et al. 1989
Yellow cotyledon	RFLP, transponsons, isozymes	h	5		Jacobs et al. 1995
Crumpled mutant	RFLP, transponsons, isozymes	h	10		Jacobs et al. 1995
Flower color	RFLP	h-s	2 (gene *D*), 10 (gene *F*), 11 (gene *P*)		Eck et al. 1993
Vine maturity	Isozymes	h	1, 2, 5	Each 7–27%	Ortiz et al. 1993a
Root development	RFLP	h-s	2, 6		Kreike et al. 1996
Tuber					
Formation	RFLP	h-s	11 loci in 1, 2, 3, 4, 5 (major locus, 27% σ^2_P), 6, 8	Each 7–14%, all 53% (60% incl. epistasis)	Berg et al. 1996a
Skin color	RFLP	h	4		Gebhardt et al. 1993
	RFLP	h-s	10 (one for anthocyanin biosynthesis and another for tissue-specific regulation of its expression)		Eck et al. 1994a
Flesh color	RFLP, isozymes	h-s	3		Bonerbiale et al. 1988
	RFLP, isozymes	h	3		Jacobs et al. 1990, 1995
Shape	RFLP	h-s	*Ro* in 10	75% genetic variance	Eck et al. 1994b
Number	Isozymes	h	5, 7	Each 18–22%	Ortiz et al. 1993a
	RFLP	4*x*	2, 4, 7, 9		Bonierbale et al. 1993
Patatin	RFLP	h	2, 7		Gebhardt et al. 1989
	RFLP		8L		Ganal et al. 1991
Weight	Isozymes	h	4, 5, 7, 8	Each 8–15%[x]	Ortiz et al. 1993a
	RFLP	4*x*	1, 2, 4, 7, 9		Bonierbale et al. 1993
Yield	Isozymes	h	2, 4, 5, 7	Each 13–29%[x]	Ortiz et al. 1993a
	RFLP	4*x*	1, 2, 4, 5, 9, 12		Bonierbale et al. 1993
			4		Kreike et al. 1996
Specific gravity	Isozymes	h	3, 7	Each 6–16%	Ortiz et al. 1993a
	RFLP	4*x*	2, 4, 5, 9, 12		Bonierbale et al. 1993
	RFLP, RAPD, isozymes	h-s	1, 2, 3, 5, 7, 11	Each 4–16%, all 39–45% (62% incl. epitasis)	Freyre and Douches 1994a,b
Reducing sugars	Isozymes	h	1, 2, 3, 4, 7	Each 5–25%[x]	Ortiz et al. 1993a
Chip color	RFLP, RAPD, isozymes	h	2 (2), 4, 5 (2), 10	Each 4–15%, all 44% (50% incl. epitasis)	Douches and Freyre 1994
Dormancy	Isozymes	h	4, 5, 7, 8	Each 10–29%[x]	Ortiz et al. 1993a
	RFLP	h-s	2 (major locus), 3, 4, 5, 8, and epistasis in 1, 9, 10, 11	Each 5–31%, all 16–48% (24–52% incl. epistasis)	Berg et al. 1996a
	Isozymes	h-s	3, 5, 7	Each 4–15%, all 36%	Freyre and Douches 1994a
	RFLP, RAPD, isozymes	h-s	2, 3, 4, 5, 7(major locus), 8	Each 4–20%, all 58% (72% incl. epitasis)	Freyre et al. 1994
Herbicide (Metrubuzin) resistance	RFLP, transponsons, isozymes	h-s	2		Jacobs et al. 1995
Tranformation competence	RFLP	h	5 linked to R_1		El-Khartboly et al. 1995

[z]Population of: h = haploids, h-s = diploid haploid-species hybrids, h-2*x* = haploid-advanced diploid hybrid, s = diploid species, 4*x* = tetraploid hybrids.

[y]Additional chromosome segments segregating in backcross generation.

[x]Loci showed overdominance for tuber yield (3), tuber weight (2), tuber dormancy (1), and reducing sugars (1).

Table 2.6. Biochemical and molecular genetic analysis of transmission of heterozygosity and 2*n* gamete formation.

Research Subject	Marker	Finding	Reference
Transmission heterozygosity	RFLP	Second division restitution (SDR) mechanism transfers 32%, while first division restitution (FDR) transfers 71% of heterozygosity of the diploid parent to its tetraploid offspring	Barone et al. 1995
	Isozymes	SDR 2*n* eggs transfer 39% of heterozygosity from diploid parents to tetraploid offspring	Douches and Quiros 1988b
	Isozymes	Synaptic mutants (FDR mechanism) transmit 82% to 98% of heterozygosity of diploid parent to tetraploid offspring	Douches and Quiros 1988c
	Isozymes	FDR and SDR 2*n* gametes transmit respectively 83% and 36% of heterozygosity of diploid parent to tetraploid offspring, while desynaptic-FDR gametes transmit 94%	Jongedijk et al. 1991a
Maximum heterozygosity test	RFLP	Depend on genetic background of parents. Important solely among adapted breeding lines: positively correlated with number of large tubers	Bonierbale et al. 1993
Mode 2*n* egg formation	Isozymes	Accurate discrimination of origin of tetraploid offspring after sexual polyploidization may allow proper comparison between FDR and SDR modes of 2*n* egg formation in potato haploids	Werner et al. 1993
	Isozymes	Postmeiotic doubling of n megaspore in *S. chacoense* generated homozygous 2*n* gametes. Only 1.8% of between gamete heterozygosity was transmitted from diploid parent to tetraploid offspring	Douches and Quiros 1988b

Two additional linkage groups were constructed with four isozyme markers, and gene-centromere distances were determined for 10 isozyme loci covering at least 8 of the 24 chromosome arms of the potato (Douches and Quiros 1987). Chiasma frequencies were investigated in male and female meiosis of desynaptic mutants with isozyme and morphological markers (Jongedijk et al. 1991a). No gender differences in genetic recombination were found for five isozyme markers that suggested that genetic exchange in both sexes was governed by the same genetic control mechanisms. Desynapsis reduces crossing over by 73% in 2*n* pollen of diploid potato (Bastianssen et al. 1996).

Isozyme-aided genetic analysis was a powerful tool in determining modes of 2*n* gametes formation (Douches and Quiros 1988b; Werner et al. 1993), transmission of heterozygosity after sexual polyploidization with meiotic mutants (Douches and Quiros 1988c; Jongedijk et al. 1991a), and the quadratic relationship between the coefficient of double reduction (α) and gene-centromere distances (Ortiz and Peloquin 1994b). None of the loci examined showed maximal equational segregation. Loci positioned at 33.3 cM from their centromere should have α values close to 1/7, i.e., chromatid segregation.

Heterozygous parents, either haploids or haploid-species hybrids, have been the most common source of offspring for mapping purposes. Markers have often been assigned to putative chromosomes based on maximum likelihood methods. Ritter et al. (1990) developed formulas to calculate the recombination frequency and information functions for different configurations when maps are based on non-inbred parents. This procedure was applied to develop potato maps based on F_1 derived by crossing heterozygous parents (Gebhardt et al. 1989).

Linkage maps based on interspecific crosses are shorter than those derived from intraspecific crosses (Gebhardt et al. 1991). This finding suggests that the degree of homology between chromosomes influences the linkage map distance. Also, genes controlling meiotic recombination during gametogenesis may explain the observed reduced recombination in some *Solanum* species and hybrids (Kreike and Stiekema 1997). Hence, relative map distances, which are calculated on the basis of recombination frequency between markers, are not only influenced by random events and the environment, but also by the genetic background.

Segregation distortion was observed around the self-incompatibility (*S*) locus in chromosome 1 in mapping populations derived from haploids, haploid-species hybrids, or *S. chacoense* (Gebhardt et al. 1991; Rivard et al. 1994, 1996). Also, the rate of recombination differed between male and female gametes (Rivard et al. 1996). Similarly, Jacobs et al. (1995) reported distorted segregation for chromosomes 1, 2, 8, and

11 (male parent) and 5 (both parents) during the development of a genetic map using second generation haploid-species hybrids. Gamete selection may explain this phenomenon. This systematic deviation from representation of alleles among the functional gametes was also observed for RFLP markers in chromosomes 2, 3, and 4 (Kreike and Stiekema 1997). There was selection against homozygous genotypes in these chromosomes, which suggested that (sub)lethal recessive genes were linked to the marker loci in respective chromosome segments.

Monogenic and polygenic (non-specific) resistance to diseases and pests have been investigated with the aid of molecular markers in haploids and diploid species-haploid hybrids (Table 2.5). Single resistance genes for specific races of late blight were located on the short arm of chromosome 5 (R_1), and a distal position of chromosome 11 (R_3, R_6, R_7). Similarly, two genes for extreme resistance to potato virus X are in the short arms of chromosomes 5 and 12, while genes for extreme resistance to potato virus Y were mapped in chromosome 11. Major genes for cyst nematode and golden nematode specific resistance were also mapped to respective segments in chromosomes 5, 7, and 9, and the resistance gene for Columbia root-knot nematode was mapped to chromosome 11. A resistance gene cluster in chromosomes 5 and 11 may exist as suggested by mapping diverse major resistance genes to similar or close chromosome segments.

Genetic analysis aided by molecular markers confirmed that quantitative variation for many characteristics was under polygenic control, as well as the complexity of specific characteristics, e.g., insect resistance in the "hairy" potato (Table 2.5). Comparison of phenotypic mean value for a quantitative characteristic between marker classes was considered as evidence of linkage between the marker and a locus coding for such phenotype. Each marker explained between 4 to 52% of quantitative trait variation for polygenic characteristics in potato. Genetic models considering all markers were able to explain up to 68% of phenotypic variation of complex characteristics. Molecular genetic models explained most of the phenotypic variation, as measured earlier by the heritability, for many polygenic characteristics. This comparison shows the power of molecular markers to dissect quantitative variation in potato.

Some quantitative trait loci (QTL) for resistance to Colorado potato beetle were common to those previously mapped for glandular trichomes (Table 2.5). This finding confirmed the role of glandular trichomes for insect resistance in potato. However, one resistance locus in chromosome 1 was not associated with trichomes. Hence, glandular trichomes account for some but not all resistance to Colorado potato beetle. Three homozygous loci with *S. berthaultii* alleles reduced oviposition by 60% with respect to heterozygous genotypes.

Common QTL influencing yield and quality characteristics were detected in diverse populations (Table 2.5). For example, markers on segments of chromosomes 2, 4, 5, 7, and 9 were linked to QTL for yield components. Similarly, QTL for specific gravity were identified in chromosomes 3, 5, and 7, whereas segments in chromosomes 2 and 4 appear to be associated with chipping ability in potato. Tuber dormancy was affected by segregation in chromosomes 2, 3, 4, 5, 7, and 8.

2. Transmission of Heterozygosity. Empirical evidence accumulated during the development of experimental tetraploids through sexual polyploidization suggests that hybrid vigor for yield could be maximized by locus multiallelism. Molecular markers confirmed that FDR 2*n* gametes are highly heterozygous when compared to SDR 2*n* gametes (Table 2.6). However, as shown by Bonierbale et al. (1993), maximum heterozygosity appears to be more important in 4*x*-4*x* crosses between adapted breeding lines than in adapted–non-adapted crosses. Furthermore, markers revealed that additive (Bonierbale et al. 1993) and non-additive (Ortiz et al. 1993a) genetic effects are associated with yield and its components in tetraploid and haploid populations, respectively.

V. THE FUTURE OF POTATO GENETIC IMPROVEMENT WITH *SOLANUM* SPECIES, HAPLOIDS, 2*N* GAMETES, AND MOLECULAR MARKERS

Potato breeders are broadening the genetic base of their breeding populations by incorporating alleles from wild species to the cultivated tetraploid gene pool through ploidy manipulations with haploids, diploid (2 EBN) species, and 2*n* gametes. This breeding technique has been incorporated as a regular germplasm enhancement tool for tuber-bearing *Solanum* spp. by the International Potato Center in Perú (Ortiz et al. 1994; Watanabe et al. 1995a) and by potato breeders in Argentina (Camadro and Mendiburu 1988), Brazil (Magalhaes-Morais and Pereira-Pinto 1996), Canada (De Jong and Tai 1991), China (Qu and Chen 1988a,b), Denmark (J. P. Nepper, Danish Potato Breeding Foundation, pers. comm.), France (Rouselle-Bourgeois and Rouselle 1995), Germany (Tellhem and Wersuhn 1990b), southern Italy (Frusciante et al. 1988), Morocco (Hilali et al., 1987), Poland (Zimnoch-Guzowska and Lojkowska 1993), Russia (Jansky 1994), Scotland (Carrol and De,Maine 1989), The Netherlands (Louwes and Neele 1989), and the United States (Peloquin et al. 1989c). Also, potato breeding with 2*n* gametes has been a successful alternative to conventional tetraploid-tetraploid breeding method in India (Birhmam and Garg 1989), Italy (Concilio and Peloquin 1991),

Northern Ireland (Watts and Lee 1990), South Africa (Visser 1991), and Turkey (Cicek and YIldIrIm 1989).

A. In situ Conservation

Agro-ecosystems are dynamic and landraces are replaced by modern cultivars. Thus, genetic erosion has occurred for decades. Consequently, species should be preserved, maintaining the genetic integrity of their natural site, as communities in stable environments. Another advantage of in situ conservation is that this approach considers the co-evolutionary dynamics among four partners: crop and wild relatives, and the pathogen populations of each species. Dynamic genetic interactions will occur for evolutionary changes in both crop and wild pathosystems (Frankel et al. 1995). The wild host will co-evolve with its resident pathogen population, whereas the pathogen population will infect the crop in response to changes in the new cultivars planted. For example, after introgressing resistance genes into new cultivars, the pathogen biotypes from the wild alternative host may invade the crop, and the new wild resistance gene will interact with the pathogen population of the crop. Thus, this conservation system may provide means for searching and testing alleles for potential durable resistance to specific potato pests and diseases, e.g., late blight in the Toluca Valley of Mexico.

B. Core Collection

Gene-banks have large and diffuse germplasm collections, which may lead to an ineffective management for rational utilization of plant genetic resources by plant breeders. For example, there are in excess of 75,000 accessions of *Solanum* species in gene-banks (van Hintum 1994). Hence, a subset of the large germplasm collection or core collection (Brown 1989) should be developed for potato. This core collection must contain chosen wild and cultivated accessions that represent with minimum redundancy the genetic variability of the whole tuber-bearing *Solanum* germplasm and closely related non-tuber bearing *Solanum* species. The sampling of germplasm for its further introgression or incorporation in the breeding pool will be facilitated by this core collection.

Core collections are assembled by grouping accessions and sampling within these groups. In potato, genetic diversity for specific crop pools or characteristics such as insect resistance are influenced by geographical distribution (Flanders et al. 1997). Moreover, unique allelic combinations are distributed unevenly among microregions and appeared to be affected by unequal rates of sexual recombination (Zimmerer and Douches 1991). Therefore, a multi-step approach will be required to develop core collection to maximize allele richness in the core during

sampling. The sampling of a potato core collection should consider relative importance of production regions, agroecological characteristics of collection sites, morphophysiological discriminating descriptors, and molecular marker data.

Breeders may start their gene search in the potato core collection. After finding the desired allele in the core collection, potato breeders should go back to the reserve collection for screening accessions of similar geographic areas for broadening their germplasm base. At the same time, available gene(s) are being incorporated into the breeding populations.

C. New Breeding Methods with Tetraploid Germplasm Derived from Sexual Polyploidization

Costs for potato breeding are reduced with ploidy manipulations. Ortiz et al. (1991b) indicated that fewer replications and locations are required to assess tuber yield in tetraploids derived from unilateral sexual polyploidization (4*x*-2*x* crosses) than those obtained by the conventional tetraploid breeding method (4*x*-4*x* crosses). Furthermore, multitrait selection for tuber yield and quality was more effective in the 4*x*-2*x* than in the 4*x*-4*x* breeding population. Ortiz et al. (1997b) suggested that reciprocal recurrent selection would be the best breeding scheme for simultaneous improvement of the tetraploid and diploid breeding populations. FDR diplandroids will be testers of the tetraploids and vice versa in this approach. Intrapopulation improvement may be done through phenotypic recurrent selection for characteristics with high heritability. The best materials from both breeding pools will then be crossed to produce tetraploid hybrids through unilateral sexual polyploidization.

Chip-processing ability of potato tubers immediately after their storage is a desired characteristic because continuous supply can be assured to the processing industry throughout the year, and costs are reduced. Tetraploid hybrids derived from 4*x*-2*x* crosses have shown their potential for potato processing in crosses with the best chipping tetraploid cultivars (Thill and Peloquin 1995). These experimental tetraploid hybrids allowed the implementation of a new breeding method for potato improvement. Testing for chipping ability of tubers harvested in the early single-hill first clonal generation was possible in their derived tetraploid offspring. This procedure could reduce the breeding program by up to four years when compared with the conventional potato breeding approach (Thill and Peloquin 1995). Yield and specific gravity of selected hybrids may be assessed in replicated plots in the second clonal generation. Furthermore, this new tetraploid germplasm provides means for avoiding inbreeding and broadens the genetic base of the conventional breeding programs.

Changing the starch composition of tubers could become a new desired goal in potato breeding. Potato starch has two chemical components: amylopectin (80%) and amylose (20%). Starch producers prefer potato cultivars with different ratios of amylopectin and amylose. A monogenic recessive mutant (*amf*) preventing the production of amylose in the starch was isolated in potato (Jacobsen et al. 1989). The *amf* allele affects the synthesis of the enzyme granule bound starch synthetase. Hence, this recessive amylose-free mutant provides a means for changing the starch composition of potato tubers. Ploidy manipulation offers the best option for the incorporation of this *amf* allele in the cultivated potato breeding pool. Nulliplex and simplex tetraploid genotypes were selected after sexual polyploidization of mutant and normal diploid genotypes (Jacobsen et al. 1991).

D. Farmers' Knowledge and Evolutionary Crop Breeding

Andean potato farmers maintain genetic diversity in their fields by cultivating more than 8000 landraces along with a few wild species (Rhoades 1994). Sometimes these indigenous people produce potato from true seed. Disease elimination, stock rejuvenation and, of course, new cultivars are some of the benefits of true seed for potato production. Genetic markers have shown a considerable gene flow between native potato cultivars and weedy *Solanum* species on small farms in the Andes (Rabinowitz et al. 1990). This finding shows the importance of cultivated and wild species in generating new landraces. Moreover, gene flow was chanelled through tuber exchange, which accounts for the absence of microgeographic differentiation in partitioning the allelic diversity (Zimmerer and Douches 1991). Hence, Andean potatoes should be regarded as a large and plastic gene pool that amplifies and renovates by outcrossing and human selection and trading of desirable forms (Quiros et al. 1992). Furthermore, a plastic gene pool could be a well-buffered system for environmental change, and may improve the durability of disease and pest resistance of current cropping systems (Robinson 1996).

E. True Potato Seed

In addition to the advantages listed above, true potato seed represents an alternative scheme to traditional production systems based on expensive or imported seed tubers. Open-pollinated true seed families are low-costing planting materials for potato production, and are virus free even though they are not uniform.

Open-pollinated seeds may result from selfing of tetraploid potato cultivars (Arndt et al. 1990). Hybrid offspring may be increased in open-pollinated true seed families by interplanting tetraploid cultivars with

diplandroid haploid-species hybrids having a genetic marker (e.g., yellow tuber flesh) (Arndt and Peloquin 1990). This scheme, plus the selection of the top 25% largest seeds for propagule production, permitted the identification of 4*x*-2*x* hybrids among open-pollinated progeny in the first clonal (or tuberling) generation.

Hybrids from 4*x*-2*x* crosses performed better for potato production from true seed than open-pollinated and selfed offspring (Schonnard and Peloquin 1991a). However, open-pollinated and S_1 generations had similar but better agronomic performance than the S_2 generation. Male gametophyte viability, positively correlated with open-pollinated fruit set, is enhanced by sporophytic heterozygosity in tetraploid potato (Ortiz and Peloquin 1994a). This finding suggests that a synthetic true potato seed cultivar propagated by open pollination may be feasible because inbreeding in advanced open-pollinated generations may be low. Furthermore, tuberlings of hybrids from 4*x*-2*x* crosses showed tuber uniformity and had higher tuber yield than the respective seedling generation (Schonnard and Peloquin 1991b). This result indicates that selection in the seedling generation may improve the performance of hybrid and open-pollinated offspring in the tuberling generation. Characteristics such as tuber color, shape, skin, and uniformity could be considered for selection in the seedling generation.

An alternative technique will be the utilization of diploid germplasm for the development of true potato seed cultivars. The commercial potential of an advanced diploid *S. phureja* population for potato production using true seed selected under long daylength was assessed by De,Maine (1996). However, tetraploid hybrids are more promising for potato production than diploids. Tuber yield of diploid hybrids was lower because of their small tuber size (Hutten et al. 1995a). Hence, Ortiz and Peloquin (1991b) proposed a new procedure for inexpensive production of tetraploid hybrid true potato seed through bilateral sexual polyploidization. In their method, diploid hybrids between haploids of *S. tuberosum* and other *Solanum* species with desirable tuber type and 2*n* gamete production are the selected parents. A male fertile self-incompatible diplogynoid with a high frequency of 2*n* eggs and no 2*n* pollen is the female parent. An unrelated male fertile diplandroid with a high frequency of 2*n* pollen will be the male parent. Also, both parents are selected for profuse flowering, and are attractive to bumblebees. Male and female parents are planted in alternate hills with bumblebees doing the pollinations. Fruit from the female plants will be harvested and seed extracted. With this method, the costs of TPS production may be reduced by more than 50% due to the elimination of emasculation, pollen collection, and hand pollination. A desired goal will be to obtain 10,000 hybrid seeds per plant, i.e., about 100 fruits with 100 seeds each.

F. Marker-assisted Introgression and Selection

Introgression of genes from wild *Solanum* species into cultivated potato may be facilitated by DNA markers. Tagging chromosome segments bearing desired alleles with DNA markers will allow their assisted genetic manipulation in potato. For example, flanking genetic markers surrounding a single resistance locus will be important tools for assisted introgression of a specific chromosome segment bearing the desired resistance allele in the breeding population.

Tightly linked molecular markers have been mapped to major resistance genes for late blight and potato nematodes (Ballvora et al. 1995; Meksem et al. 1995). Researchers at the Max Planck Institute (Germany) converted restriction fragment length polymorphism (RFLP) markers to DNA marker systems testable by a polymerase chain reaction (PCR) assay (Gebhardt 1994). This PCR-assay was a successful breeding tool for assisted selection at the seedling stage. Plants carrying the resistance genes were distinguished from the susceptible plants. However, a precise knowledge of which genes exist in parental material will be required to apply a common marker-assisted introgression system to all diploid and tetraploid breeding populations (Newohner et al. 1995).

Simple sequence repeats (SSR) or microsatellites are a group of repetitive DNA sequences (up to 10 bases) often tandemly arranged, and exhibiting uniform sequence motifs in the eukaryotic genome. Variation in the length of DNA fragments containing simple repetitive sequences results in simple sequence length polymorphisms (SSLP), which are important tools for marker-aided analysis. Recently, SSLP analysis has been used to determine genetic relationships in cultivated potato (Provan et al. 1996a), and among potential intraspecific hybrids of potato (Provan et al. 1997). Also intermicrosatellite amplification with two 5′-anchored repeat primers provides a means for phenetic analysis in and genotyping of tetraploid potato cultivars (Provan et al. 1996b). Furthermore, SSR detected the highest amount of polymorphism, as measured by the diversity index, when compared to amplified fragment length polymorphism (AFLP) and randomly amplified polymorphic DNA (RAPD) (Milbourne et al. 1997). PCR-based markers such as SSR are based on a high resolution assay that is amenable to automation. Hence, time and associated costs for marker-assisted selection in potato breeding may be saved greatly with SSLP.

Markers linked to QTL are inconsistent across populations and environments (Bonierbale et al. 1993; Freyre and Douches 1994b; Ortiz et al. 1993a). This was not surprising, since phenotypic variation depends on the genotype and often phenotypes are influenced by the genotype-by-environment interaction (GE). The environment does not affect the marker phenotype. However, the GE affects the phenotypic variation of the characteristic under investigation, thereby changing the relative magnitude association marker-QTL measuring. Therefore, candidate marker models for assisted selection, especially for characteristics with low heritability, must be validated in independent populations and across environments. Furthermore, a mixed phenotypic-marker selection index could improve assisted selection with genetic markers. This selection index may allow selection of several characteristics simultaneously.

G. Potato: A Model System for Breeding Other Vegetatively Propagated Polysomic Crops

This review has shown the success of ploidy manipulations in potato breeding. This general approach, or with some modifications (Fig. 2.5), could be extended to other vegetatively propagated polysomic crops (Peloquin and Ortiz 1992). Major gains on yield and quality for root and tuber crops will improve the agricultural systems, especially in the tropical developing world.

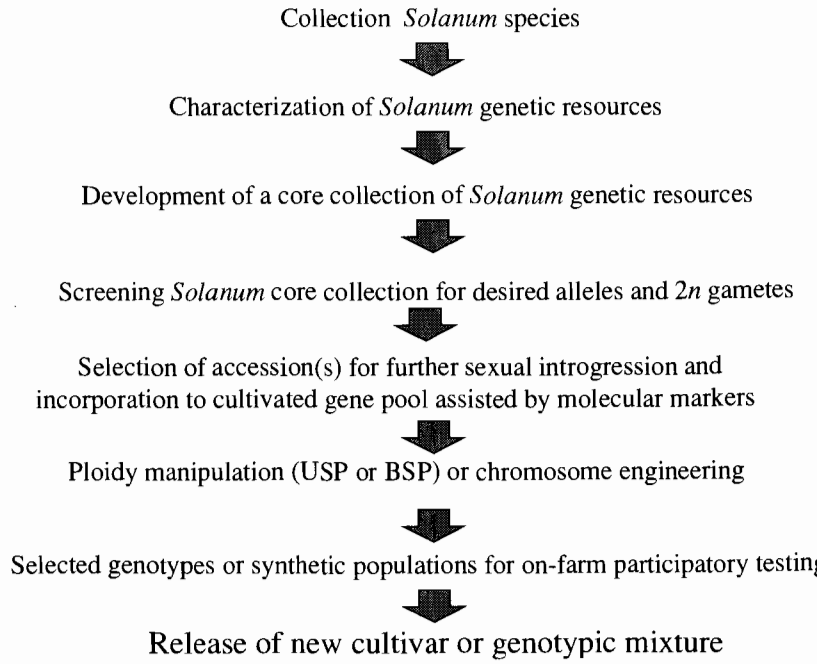

Fig. 2.5. Scheme for the utilization of *Solanum* genetic resources in sexual potato breeding. USP = unilateral sexual poliploidization, BSP = bilateral sexual poliploidization.

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