Genetics and Breeding of Potato with Special Reference to Some Breeding Problems in Developing Countries

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1. Introduction

Potato (*Solanum tuberosum* L.) is an ancient South American food staple which has spread worldwide and ranks among the world's major food crops along with rice, wheat and corn. Hawkes (1967; 1978) elegantly described the history of potato development and spread from the time it was moved from its center of origin, the Andean mountains of South America, to the present where it has gained the status of a principal foodstuff of great economic importance.

Relative to the cereals, potato is, by a large measure, a more remarkable crop because it combines two of the most important attributes of a staple food—high yield per unit area per unit time with a good balance of carbohydrates, protein and minerals. By itself, potatoes show a protein biological value of 98, a close second when compared to the reference protein of eggs at 100 (cf. Anon, 1980a). Its average energy production per day is second only to sweet potatoes and higher than rice, corn or cassava. Potato protein production per hectare per day is estimated at 1.3 kilograms, the highest among major tropical food crops. Its short growing period provides another advantage: at 125 days average, it is fast growing and can thus fit easily into most existing cropping systems.

The highest production levels on per capita basis are in the northern latitude countries of Europe and North America, and not surprisingly, these are the areas where the contribution of potato to human caloric intake is greatest. In recent years, production has declined in several West European countries mainly due to a gradual reduction in production areas (Horton, 1978). On the other hand, for the developing countries as a group potato production has grown at a faster pace than production of most other food crops (Fig. 1).

As a general trend in developing regions, potato yields have kept pace with the increases in cereal yields (Horton, 1987). Improvements in varieties, seed systems, and post-harvest technology have helped bring down the cost of producing potatoes in the developing areas. Indeed, the balance of world potato production is now gradually shifting from developed to the developing countries and from temperate to the tropical countries. The depressed potato yields in other areas of the developing world may be continually attributed to the persistently low levels of potato technology—poorly adapted cultivars, inavailability of clean seed, inadequate pest and disease control practices, lack of appropriate storage facilities, insufficient agronomic practices knowhow, etc. (Anon, 1976b).

It is not within the scope of this lecture to discuss the above problems but a brief reference to the aspects of cultivar development in developing countries is given here as a prelude to the main theme—genetics and varietal improvement of potato. Further discussions are given in later sections.

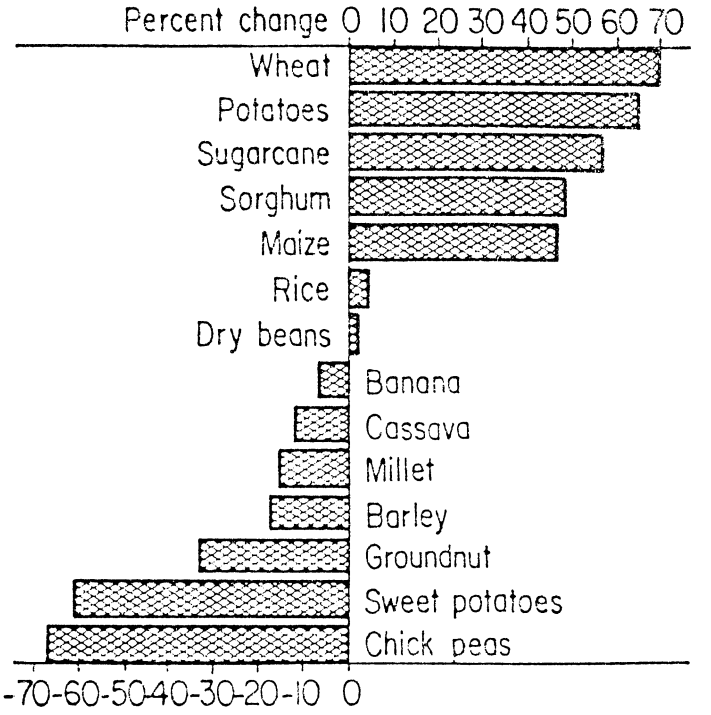


Fig. 1. Change in per capita production of major food crops in developing market economies, 1961/65-1982/84. Source: FAO, Production yearbook 1976; 1984 (Rome, 1977; 1985).

Most potato cultivars grown in developing countries were bred in the temperate zones. In the absence of any breeding program to serve the local variety requirements, there is simply no recourse but to find the most suitable types from among introduced cultivars. The climatic conditions of the temperate regions are however far different from those in developing countries (especially in the tropics where most of these countries lie)—variations in daylength, temperature, rainfall and other abiotic factors are very pronounced. Logically therefore, the varieties from temperate countries are generally unadapted when grown in the tropics even if the temperature stress is significantly reduced by concentrating production in the cooler highlands.

Several developing countries of the Asian region have had, or are now interested on varietal improvement programs. As a matter of fact, countries such as Indonesia, Philippines, Thailand, Sri Lanka, and Papua New Guinea have established a regional cooperative linkage under the aegis of SAPPRAD (Southeast Asian Program on Potato Research and Development). In this, potato breeding to serve the needs of member countries is an important component. The role of the International Potato Center (CIP) in terms of availing improved germplasm (but not named cultivars) should significantly improve the chances of finding better adapted varieties for the tropical countries.

It is therefore the objective of this article to provide tropical potato breeders with sufficient background information relevant to potato breeding and consequently, to present

the various techniques of breeding, traditional and unconventional, which have been practised or are currently being explored. In the process, it is hoped that the body of information presented herein will provide some useful guidelines.

2. Biosystematics of Potato and the Range of Exploitable Diversity

Much of the breeding in potato since it was brought into Europe in the early 16th century has been simply a continuous reassortment of the variability contained in the few, original Andigena introductions. Still, the evolution of subspecies Tuberosum from those limited introductions through the combined forces of natural and human selection (Salaman, 1964; Salaman and Hawkes, 1949; Salaman, 1954; Hawkes, 1967) is a remarkable proof to the enormous store of genetic variation that those clones carried. There were only a few occasions in the past when genetic diversity had been significantly added to the present day Tuberosum gene pool, such as the importations of new Andigena germplasm into New York by Rev. Chauncey Goodrich between 1848 to 1852. Rough Purple Chile, one of those clones imported from Panama, figured in the pedigree of many later varieties by way of its descendant, Early Rose.

Overall, the progress that has been attained by the 19th century potato breeders was made on a very narrow genetical base (Simmonds, 1969). When further decimation of the gene pool by the late blight epidemics of the 1840's is taken into account, it becomes even more remarkable that the limited genetic materials have been extremely rewarding and this must be due in large part to the variability concealed by heterozygous clones.

It is reasonable to assume that the diversity contained in the original Andigena introductions into Europe is but a small portion of what existed at the Andean center of origin even if recorded introductions are taken as only a token of the actual number (Cardenas, 1966). Roughly, less than one percent of the genetic variability of *solanum* has been utilized in the development of existing varieties of potatoes (Anon, 1974). A brief biosystematic treatment of the potato should serve to stress the above point as well as emphasize the fact that an enormous range of genetic diversity is indeed available for potato breeders to exploit further.

The potato of commerce that we all know belongs to *Solanum tuberosum* L., one of eight cultivated species. Apart from the cultivated species, 154 wild species of potato are recognized (Hawkes, 1978). The rest of the genus *Solanum*, an extremely large genus comprising of some 2,000 species, are non-tuber bearing forms (although two non-tuber bearing series, *Juglandifolia* and *Etuberosa*, are included under Section Petota to which the potato species belong on the basis of key morphological traits).

Table 1 shows the recognized series under Section Petota, the number species within each series, the chromosome races when available, and traits that have so far been identified in some of the better known species. The limited information concerning valuable traits of some species given by Hawkes (1978) were supplemented with those provided by Anon (1974). Additional information, where specifically sought, may be obtained from Bulletin 533 of the College of Agriculture and Life Sciences, University of Wisconsin, Madison, Wisconsin 53706, U.S.A., entitled "Inventory of tuber-bearing *Solanum* species" by Ross and Rowe (1966). This bulletin is very useful in listing sources of resistance to a number of diseases, where known, in the IR-1 potato Collection in the United States.

As may be noted, 18 series are recognized of which series Tuberosa is the largest. Series Tuberosa itself is further subdivided into cultivated and wild species. The cultivated forms occur at four ploidy levels, tetraploids being the major cultivated group. The frost-resistant species, *S. ajanhuiri*, *S.* x *goniocalyx* (*x* indicates species hybrid form) and *S.* x *curtilobum* are grown at 3,000 to 4,000 m above sea level in the Andean mountains of South America. *S. tuberosum* ssp. *andigena*, *S. stenotomum* and *S. goniocalyx* are mostly grown at 2,500 to 3,500 m. *S. phureja* , on the other hand, are well adapted to the warm temperate frost-free lower valleys of the eastern Andes. As cited earlier, *S. tuberosum* ssp. *tuberosum* evolved from ssp. *andigena* by human and natural selection forces to adapt them to long days in lower altitudes of higher latitude regions of the world and to some extent, although not considered fully well-adapted, to higher altitudes in tropical countries.

In comparison to the cultivated species, wild species thrive in a wider range of habitats and have a broader latitudinal distribution. Apart from their greater climatic adaptability, wild species generally show greater adaptation to pests and diseases oftentimes lacking among the cultivated forms, Their potential value in breeding has not been fully exploited however. Nonetheless, a few outstanding examples of their useful contribution to the *tuberosum* gene pool are already known—major R-genes for late blight resistance from *S. demissum*, resistance to PVY from *S. stoloniferum* and *S. chacoense*, and frost resistance from *S. acaule*. There are of course still a great number of important traits that remain untapped (see Table 1). The breeders apathy towards the use of wild species for breeding purposes is not entirely unfounded (see section 5.1.4.2). In some cases, breeding barriers between cultivated and wild species do exist although, as a whole, they are known to hybridize well enough so that enforcing the gene flow from many wild species to the cultivated types is not an impossible task. Majority of wild diploid species will hybridize easily with cultivated diploids. Even tetraploid x diploid crosses can be accomplished, although with slight difficulty.

Hawkes(1978) cited several forms of interbreeding barriers in natural populations: temporal barriers such as difference in flowering time between two species with overlapping ecological distribution; clear cytogenetical barriers resulting in F_1 hybrid sterility; and F_2 hybrid breakdown giving rise to F_2 plants of low fertility and viability. In general, there are two main groups of potato which are difficult to cross. The first group includes the series Morreliformia, Bulbocastana and Pinnatisecta. The second consists of series Commersoniana, Circaeifolia, Conicibaccata, Piurana, Acaulia, Demissa, Longipedicellata, Cuneoalata, Megistacroloba and Tuberosa. Thus far, there have been demonstrated instances where, through proper manipulations such as the use of bridging species, hybridization barriers between certain species from the two groups have been broken (Dionne, 1963; Hermsen and Ramanna, 1973). Hawkes (1978) predicted that most, if not all, of the wild potato species (with the probable exception of non-tuberiferous series Juglandifolia and Etuberosa which lie outside any of the potato crossability groups) will sooner or later be brought into the gene pool of the cultivated potato, *S. tuberosum*. If such is the case, the already large gene pool will further expand thereby increasing the range of exploitable diversity available to the breeders.

Table 1. Biosystematic groupings in the genus *Solanum* Section Petota, chromosome numbers, and some recognized valuable characters of a few well-known species (modified after Hawkes, 1978)

Series	Species Within Series	Chromosome Races (somatic number)	Some Valuable Traits and Other Remarks
I. JUGLANDIFOLIA (non-tuber bearing)	- *juglandifolium, lycopersicoides, ochrantum, rickii*	24	not well-studied
II. ETUBEROSA	- *etuberosum, brevidens, fernandizianum*	24	not well-studied
(non-tuber bearing)	- *palustre, subandinum*	?	*palustre* rare or extinct
III. MORRELIFORMIA	- *morreliforme*	24	not well-studied
IV. BULBOCASTANA	- *bulbocastanum* (3 subspecies)	24,36	resistance to late blight and leafhopper
	- *clarum*	24	not well-studied
V. PINNATISECTA	- *brachistotrichum, michoacanum* (sp. hybrid), *stenophyllidum*	24	not well-studied
	- *cardiophyllum* (3 subspecies), *jamesii*	24,36	resistance to late blight in *cardiophyllum*
	- *hintonii, nayaritense*	?	not well-studied
	- *sambucinum* (sp. hybrid), *trifidum, pinnatisectum*	24	resistance to late blight in all species; leafhopper resistance in *pinnatisectum*
VI. COMMERSONIANA	- *yungasense* (2n =24), *calvescens* (2n=36)	24,36	not well-studied
	- *tarijense*	24	resistance to late blight, early blight, *Verticillium* wilt, aphids
	- *chacoense* (2 subspecies)	24	resistance to virus Y, blackleg, early blight, *Verticillium* wilt, cyst nematode (?), aphids, Colorsdo beetle
	- *commersonii* (2 subspecies)	24,36	moderate frost resistance, some resistance to late and early blight
VII. CIRCAEIFOLIA	- *capsicibacatum, circaeifolium*	24	not well-studied
VIII. CONICIBACCATA	- *agrimonifolium, colombianum, longiconicum, oxycarpum*	48	not well-studied

Series	Species Within Series	Chromosome Races (somatic number)	Some Valuable Traits and Other Remarks
	- *albornozii, ayacuchense, buesii, multiflorum, paucijugum, pillahuatense, tundalomense, urubambae, villuspetalum, woodsonii*	?	not well-studied
	- *moscopanum*	72	not well-studied
	- *chromatophilum, jaenense, laxyssimum, neovargasii, violaceimarmoratum*	24	some frost resistance in *chromatophilum*; others not well-studied
IX. PIURANA	- *solicii, yamobambense*	?	not well-studied
	- *agrolossum, paucissectum, piurae*	24	not well-studied
	- *tuquerrense*	48	self-incompatible tetraploid
X. ACAULIA	- *acaule* (4 subspecies)	48,72	resistance to ring rot, high frost resistance, some resistance to late blight and cyst nematode (?)
XI. DEMISSA	- *brachycarpum, iopetallum*	72	not well-studied
	- *demissum, guerroense, hougasii*	72	late blight resistance in all but especially *demissum* (also carries PVY and leafhopper resistance); PVY resistance in *hougasii*
	- *edinense* (sp. hybrid; 2 subspecies), semidemissum (sp. hybrid ?)	60	resistance to late blight
XII. LONGIPEDICELLATA	- *fendleri* (2 subspecies), *jertingii, papita, polytrichon, stoloniferum*	48	late blight resistance in *stoloniferum* and *polytrichon*; virus resistance in *fendleri* and *stoloniferum* (also flea beetle resistance)
	- *vallis-mexice* (sp. hybrid)	36	not well-studied
XIII. POLYADENIA	- *lesteri, polyadenium*	24	resistance to late blight and aphids in *polyadenium*
XIV. CUNEOALATA	- *infundibuliforme*	24	possible drought resistance

Series	Species Within Series	Chromosome Races (somatic number)	Some Valuable Traits and Other Remarks
	- *anamotophilum*	?	possible drought resistance
XV. MEGISTACROLOBA	- *chavinense, hastiforme, toralapanum*	24	not well-studied
	- *dolichocremastrum, hawkesii, huanocense*	?	not well-studied
	- *boliviense, megistacrolobum, raphanifolium, sanctarosae, sogarindinum*	24	frost resistance in all species; also resistance to cyst nematode in all except *raphanifolium* and *sogarindinum*
	- *bruecheri* (sp. hybrid)	36	not well-studied
XVI. INGAEFOLIA	- *ingaefolium*	?	not well-studied
	- *rachialatum*	24	not well-studied
XVII. OLMOSIANA	- *olmosense*	24	not well-studied
XVIII. TUBEROSA			
a. Wild Species	- *abancayense, alandiae, amabile, ambosinum, andreanum, brevicaule, cajamarcense, coelostipetalum, colominense, cyanophyllum, doddsii* (sp. hybrid), *jalcae, lobbianum, minutifolium, mochicense, mollepujroense, orophilum, paramoense, regularifolium, rhompodeilanceolatum, sandemanii, scabrifolium, suffrutescens, torrecillasense, trinitense, velardei, virgultorum*	?	cyst nematode resistance in *andreanum* and *brevicaule*; frost resistance in *jalcae*; *others* not very well-studied
	- *berthaultii* (sp. hybrid), *bukasovii, canasense, candolleanum, cantense, chancayense, chiquidenum, contumazaense, gandarillasii, gracilifons, huncabambense, humetophilum, hypacrarthum, immite, kurtzianum, lepthophyses, lignicaule,*	24	aphid resistance in *berthaultii*; cyst nematode resistance in *kurtzianum, leptophyses, multidissectum, spegazinii, sparsipilum, vernii*; frost resistance in *bukasovii, canasense, multidissectum, spegazinii*, vernii;

Series	Species Within Series	Chromosome Races (somatic number)	Some Valuable Traits and Other Remarks
	marinasense, multidissectum, multiinterruptum, neoweberbauri, pampasense, pascoense, rechei (sp. hybrid), *setulosistylum, spegazinii, sparsipilum, vernii, verrucosum, vidaurrei, weberbaueri, wittmackii*		late bligh resistance in *kurtzianum, spegazinii, vernii, verrucosum*; drought resistance in *gandarillassii, kurtzianum, sparsipilum*; blackleg resistance in *setulosistylum*; others not well-studied
	- *maglia, microdontum* (2 subspecies), *medians, venturii)*	24,36	resistance to cyst nematode in *venturii* and *microdontum* (also to PVY and late blight)
	- *acroscopium, sucrense*	48	resistance to cyst nematode in *sucrense*
	- *goularyi*	24,48	not well-studied
	- *oplocense*	24,48,72	resistance to cyst nematode
b. Cultivated pecies 1. Diploids	- *ajanhuiri, goniocalyx, phureja, stenotomum*	24	frost resistance in *ajanhuiri, goniocalyx*, and some in *stenotomum* ; resistance to bacterial wilt, *Verticillium* wilt, blackleg, and late blight in *phureja*
2. Triploids	- *chaucha* (sp. hybrid), *juzepcaukii* (sp. hybrid)	36	immunity to virus X and wart, late blight resistance, high dry matter and protein in *chaucha*; resistance to wart, hypersensitivity to virus X, resistance to frost, early blight and cyst nematode in *juzepczukii*
3. Tetraploids	- *tuberosum* (ssp. *tuberosum, andigena)*	48	*tuberosum* is the cultivated form in most areas of the world except South America where the *andigena* form is grown; many important traits of commercial

Series	Species Within Series	Chromosome Races (somatic number)	Some Valuable Traits and Other Remarks
			significance already in *tuberosum*; some resistance to late blight, immunity to PVY, resistance to PVX, PVS, common scab, wart, *Verticillium* wilt, aphids, leafhoppers, cyst nematode, root knot nematode, etc, in ssp. *andigena*
4.Pentaploids	- *curtilobum* (sp. hybrid)	60	some frost resistance; resistance to late blight, wart, early blight, *Fusarium*, high dry matter and high protein

3. Reproductive Systems of Potato: Consequences in Breeding and Production

The breeding system of a particular species largely dictates the breeding methods to be used (Table 2). Even within a defined system, breeding approaches may vary in accordance with the primary objectives of the plant breeder and / or the nature of the parents chosen in a hybridization program. For example, backcross breeding is more appropriate than other methods when one of the parents (usually termed the donor) is a commercially undesirable type but carrying an important trait lacking in the other parent (usually termed the recipient or recurrent parent), normally a popular cultivar. .

Potato reproduces both sexually and vegetatively (via tubers). The sexual system affords the plant breeder with a reliable scheme to generate variability from which new cultivars may be derived. It has been through this system that most, if not all, present day cultivars had been and still are being produced. Bud sports arising through somatic mutations have, on several occasions, improvement of potato is rather small (Van Harten, 1978).

Most diploid potato species (both cultivated and wild) are outbreeders. This mating system is obligatory because of the presence of a genetically controlled self-incompatibility mechanism. The incompatibility is of the gametophytic type and, as in many other crop plants exhibiting the same system, due to a series of S-alleles. Self-compatible species such as *S. brevidens*, *S. etuberosum* and *S. morreliforme* provide exceptions to the usual rule of self-incompatibility among diploid species (Hawkes, 1978).

In contrast, most pollen-fertile tetraploid and hexaploid species are self-compatible. The presence of S-alleles among cultivated tetraploids (sub-species *tuberosum* and *andigena*) has been proved by investigations of dihaploid derivatives (Cipar, Peloquin and Hougas, 1964). Although self-pollination is possible, the cultivated tetraploids still behave basically as outbreeders and exhibit inbreeding depression upon selfing. Krantz (1946) studied the effect of inbreeding on tuber yield and reported a 17% yield reduction in the first (I_1) inbred

generation. By the I_6 generation, the actual yield of the inbred family was only 19% relative to the mean F_1 performance.

The breakdown of the self-incompatibility mechanism at the higher ploidy levels in potato has been suggested to be due to competitive interaction (or mutual weakening) of S-alleles. This theory was advanced by Lewis (1954) and further supported by Arasu (1968). Cipar (1964) found however a high incidence of self-compatibility among normally self-incompatible hybrids of dihaploids with *S. phureja*, implying that the self-compatibility in cultivated tetraploids is due to genes modifying the action of S-alleles rather than competitive interaction. Although belonging to another species, *S. tuquerrense* in the series Piurana is a curiously self-incompatible tetraploid and provides an exception to the self-compatibility rule in the tetraploid group (Hawkes, 1978). Moreover, its maintenance of incompatibility at the polyploid level does not conform with the theory of competitive S-alleles interaction.

Several important consequences of vegetative propagation in potato breeding were given by Howard (1970; 1978). Asexual propagation allows maintenance of the genetic identity of individuals barring rare somatic mutations. Therefore, every seedling in the breeding program can be a potentially new variety. The use of other methods such as wide crosses, mutation breeding, and polyploidy breeding is similarly facilitated by asexual propagation. Any promising individuals therefrom can easily be maintained and/or propagated.

Asexually-propagated crop species are generally highly heterozygous. Potato is not an exception. When two cultivars are crossed, segregation for a wide array of traits is immediately apparent in the hybrid seedlings. While this condition provides breeders with a slight temporal advantage, selection at least for some traits being possible in the F_1 generation, the genetic consequence of heterozygosity far outweighs the time gained. The highly heterozygous nature of potato cultivars means that, when hybridized among each other, they can transmit their good characteristics only to a very small proportion of the progenies. Therefore, growing a large number of hybrid progenies is an absolute prerequisite to maximize the chances of isolating desirable recombinants.

Debilitating virus diseases usually accumulate in vegetatively propagated crop plants especially if no measures are taken to minimize virus infection. Degeneration of potato varieties is a well-known problem. Fortunately, virus-infected cultivars can now be routinely "cleaned" by meristem culture methods (Morel, 1964; Kassanis, 1965). However, such procedures are ineffective unless combined with good seed production practices such as the use of appropriate seed districts, efficient pest and disease management, effective seed certification scheme, etc. Virus diseases, except potato spindle tuber viroid (Diener, 1971), are non-transmissible by true seeds. Every new seedling therefore arising from true seeds is practically virus-free and it is the responsibility of breeders to insure that they remain so through the different stages of selection and clonal multiplication. Unless this is kept in mind, valuable genotypes could easily be selected against on account of virus-infection.

Other disadvantages to the breeder accruing from the vegetative reproduction of the potato (Howard, 1978) are as follows:

(a) varieties may not flower or even if they do, could be pollen sterile (ovule sterility is rare) and therefore, their use is restricted in the crossing programs;
(b) large amounts of materials must to be stored under ideal conditions;
(c) transport of tubers is much more difficult than that of seeds;
(d) clonal materials do not store as easily as seeds and must be grown each year ;
(e) multiplication rate is much slower than by seeds.

Table 2. Genetic architectures and breeding methods applied to different breeding systems (partly modified from Briggs and Knowles, 1967)

Characteristic or Breeding Technique	Breeding System		
	Self-pollinating species	Cross-pollinating species	Facultative asexual
a. GENETIC ARCHITECTURE OF NATURAL POPULATIONS			
Genotype of the sporophyte	homozygous	heterozygous	heterozygous
Genotype of the gametes from a single plant	similar	different	different
Progeny of a single plant	homogeneous	heterogeneous	heterogeneous
Self-incompatibility	none	frequent	yes
Inbreeding depression	none	usual	yes
b. BREEDING TECHNIQUE			
Introduction	yes	yes	yes
Pure line selection	often	only as parents for hybrid varieties	proposed for creating hybrids but not fully developed
Mass selection	occasionally	frequently	occasionally for population improvement
Pedigree breeding	yes	no	yes, but not in the context of the method as applied to self-fertilizing species
Backcross breeding	yes	yes	yes (modified method)
Hybrid varieties	occasionally	yes	proposed but not fully developed
Recurrent selection	occasionally	yes	occasionally for population improvement

[a] Using cultivated potato tetraploids as example; facultative asexuals are species which normally reproduce vegetatively but capable of sexual reproduction, e.g., potato.

Another obvious disadvantage of vegetative propagation may be added to the above—the constant fear of introducing tuber-borne viral, fungal and bacterial diseases, and pests (including nematodes) constitutes a serious deterrent to free germplasm exchange among breeding programs. The use of tissue culture (Roca *et al.*, 1979) may alleviate this problem and enable a more widespread transfer of potato genetic materials especially those coming

from South America, the widespread transfer of potato genetic materials especially those coming from South America, the recognized center of diversity.

4. Genetic Basis of Some Morpho-Physiological Traits and Resistance to Diseases

Howard (1970) reviewed previous works in potato genetics with emphasis on the cultivated tetraploids. In addition, previous surveys have been done, all published in the journal "Bibliographia Genetica": Fruwirth (1925) in Vol. 1 pages 315-362; Swaminathan and Howard (1953) in Vol. 16, pages 1-192; and Howard (1960) in Vol. 19, pages 87-216.

This section is largely a summary of information provided by Howard (1970) but supplemented by more recent literatures whenever available. It must be understood that there are many gaps in our knowledge of potato genetics primarily because potato is not an ideal specimen for genetical research—it is a tetraploid which introduces some complexity to interpretation of genetic data; moreover, potato has a large number of small chromosomes; it is rather bulky and requires considerable expenditures of land or greenhouse space to raise an adequate population size; being propagated vegetatively, it also becomes too quickly infected by degenerative viral diseases.

The advent of dihaploids (haploids derived from tetraploids) should greatly facilitate genetic studies because of the relative genetic simplicity at this ploidy level. Genetic stocks are also being used to establish linkage relations and in crosses with trisomics to situate genes to particular chromosomes (Hermsen *et al.*, 1973). These trisomic sets have already been established in *S. tuberosum* (Yeh and Peloquin, 1965; Ramanna and Wagenvoort, 1976). Therefore, the future has in store the filling up of gaps in our knowledge of potato genetics.

4.1 Tuber flesh, stem, and sprout pigmentation

Anthocyanin pigments in potato are found in flowers, stem, sprout and in some cases, in flesh as well as skin of tubers. At least six major genes controlling anthocyanin pigmentation in tetraploid cultivated potatoes are known (Salaman, 1926; Sirks, 1929; Asseyeva and Nikolayeva, 1935; Lunden, 1960; Howard, 1970). Four of these genes, designated by symbols R, E, D, and P, act independently in controlling sprout pigmentation. Nearly all varieties have one or more of the four genes and therefore, it is very infrequent to find unpigmented sprouts. These same four genes may be involved in the control of stem color.

Krantz (1922) concluded that purple flesh of cv. Congo Black was due to a single dominant gene based on the 3:1 purple to white fleshed ratio among its selfed progenies. A more complicated situation was observed by Muller (1923) who observed a 9 pigmented : 7 white ratio upon selfing a pigmented variety. Only white fleshed types resulted in crosses with a white variety. Complementary genes C and I were postulated for flesh color along with an inhibitor, gene Z.

4.2 Tuber shape

Salaman (1926) suggested that tuber shape was conditioned by a single gene for length. Long shape was dominant to round tubers which bred true to type. Bartosch (1930), Rathlef and Siebeneck (1934), and more recently Schick (1956) disagreed with the single gene theory and suggested instead that several genes are likely involved to explain the distribution of shapes in segregating families studied.

4.3 Depth of eyes

Although there was no complete dominance among hybrid progenies, deep eyes was largely dominant to shallow eyes (Salaman, 1912; Heribert-Nilsson, 1913). East (1910) and Black (1930) suggested otherwise and postulated a genetic control by more than one gene. According to Huber (1930), two complementary genes were involved in shallow eye expression.

4.4 Tuber flesh color

Deep yellow flesh was found to be dominant to white and controlled by a single gene and modifiers with small effects (Fruwirth, 1912; Salaman, 1926). Schick (1956) and Engel (1957) agreed with this theory although certain findings such as those by Heribert-Nilsson (1913) and Black (1930) seemed to refute the early theory.

4.5 Growth habit

At least three genes are involved in the genetic control of growth habit, with normal upright dominant over prostrate (Salaman and Lesley, 1920). Procumbent (intermediate between extremes of growth habit) was recessive to upright and monogenically controlled.

4.6 Glycoalkaloids

The inheritance of major glycoalkaloids, the bitter principle in tubers of wild potato, *S. chacoense*, identified by thin-layer chromatography, has been studied (McCollum and Sinden, 1979). Monogenic segregations (3 : 1 in F_2 and 1 : 1 in BC_1) were obtained for presence : absence of glycoalkaloids solanine, chaconine, and commersonine. In simultaneous segregation of the three glycoalkaloids, the following interpretations were suggested to explain the observed results:

(a) solanine and commersonine are determined by alternative co-dominant alleles at a single locus;
(b) the major gene for chaconine segregates independently of the sola nine/commersonine locus;
(c) a recessive gene linked with commersonine allele was epistatic to the chaconine gene causing production of b-chaconine instead of the usual a-chaconine.

The F_2 fits the ratio 3 : 6 : 3 : 1 : 2 : 1, seen as combining the 1 : 2 : 1 segregation of solanine : solanine + commersonine : commersonine and the 3 : 1 segregation for presence : absence of chaconine.

4.7 Tuber number, size, yield and time to maturity

These characters are lumped here because as major components of yield, number and size of tubers, and growth duration are highly influenced by daylength. For example, tuber initiation is earlier under short days than under long days and tuber yield in relation to weight of haulm (vegetative portion) is much higher under short days. Maturity is also shortened under short days. It is therefore important to realize that any results on inheritance of time to maturity and yield must consider the large influence of photoperiod (Howard, 1970).

Engel (1957) studied tuber number, size and yield, and concluded that yield is difficult to determine for large number of seedlings, even if difference in maturity and environmental responses are disregarded. The accuracy of yield determinations depends on large samples, determination based on single plants having an extremely high error.

Schick (1956) and Moller (1956) studied the frequencies of early maturing seedlings under long day conditions from crosses of two early maturing varieties and concluded that maturity depends upon a number of genes and varieties are heterozygous for most of these.

4.8 Resistance to late blight

Late blight, caused by *Phytophthora infestans* (Mont.) de Bary, attacks both the foliage and the tubers. A typical symptom on the leaves is shown in Figure 2 below:

The hypersensitive type of foliage resistance to late blight, controlled by R-genes, has been widely studied. The main source of this type of resistance is the wild Mexican hexaploid species (2n = 72), *S. demissum*. To date, 11 major R-genes are known.

Major R-gene resistance is race-specific and very unstable in the face of a highly variable pathogen (Section 5.1.4.7.1.). Black *et al.* (1953) established the relation between the genes for hypersensitivity and the races of the pathogen. The scheme is internationally accepted and based from the original work of Black (1952). A sample of this nomenclature is given in Table 3.

The hypersensitive resistance type is considered of limited importance because of its instability. As new resistance genes and their combinations are bred, it does not often take long for new races capable of attacking them to arise. Greater interest is now focused on another type of resistance called field resistance or non-race specific resistance. In theory and practise, this type of resistance is more longer - lasting than race-specific resistance. Black

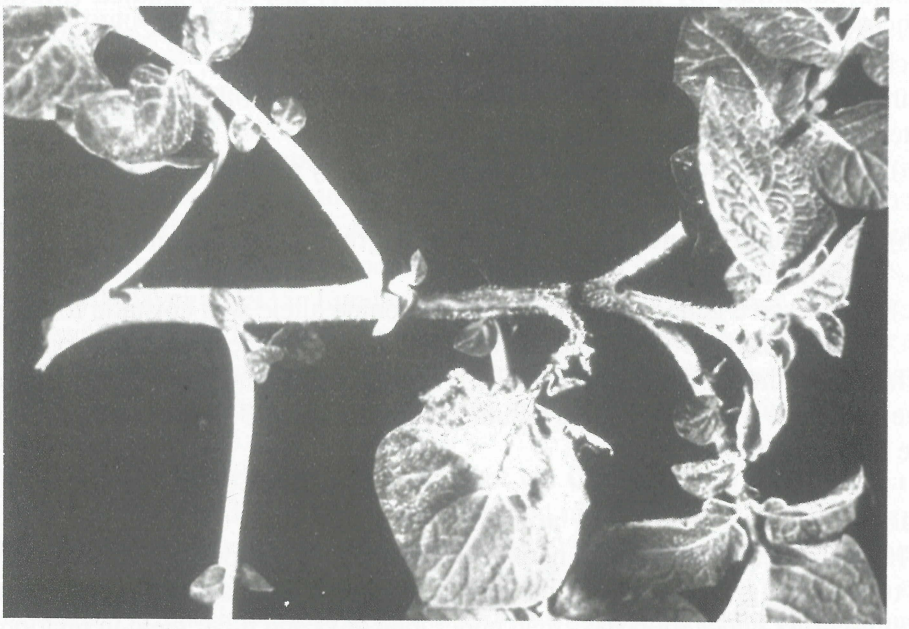


Fig. 2. Typical late blight symptoms on potato leaves.

(1960; 1972) suggested that field resistance is controlled by many genes (see Table 7). Sources of this type of resistance have been found also in *S. demissum* and other species, both cultivated and wild (section 5.1.4.7.1).

Table 3. A sample of the international scheme on nomenclature of major R-genes for resistance and races of *Phytophthora infestans* (after Black et al., 1953).

Potato genotype	Phyisiological race of *P. infestans* [a]							
	0	1	2	3	4	1,2	1,3	1,4
r	S	S	S	S	S	S	S	S
R_1	R	S	R	R	R	S	S	S
R_2	R	R	S	R	R	S	R	R
R_3	R	R	R	S	R	R	S	R
R_4	R	R	R	R	S	R	R	S
R_1R_2	R	R	R	R	R	S	R	R
R_1R_3	R	R	R	R	R	R	S	R
R_1R_4	R	R	R	R	R	R	R	S

[a] R = resistant; S = susceptible

4.9 Resistance to bacterial wilt

Bacterial wilt is caused by *Pseudomonas solanacearum* E.F. Smith. Figure 3 shows an infected potato plant. Resistance has been identified in *Solanum phureja* although apparently not common (Thurston and Lozano, 1968). Reaction to the pathogen at the diploid level appears to be conditioned by three dominant and independent genes plus modifiers (Rowe and Sequeira, 1970; Rowe *et al.*, 1972). At the tetraploid level, two dominant genes have been postulated to confer resistance (Anon, 1979). In addition, a dominant gene for susceptibility which exerted a dosage-dependent epistatic effect on the two dominant resistance genes was also suggested by the tetraploid segregation data. The dominant resistance genes were probably identical to those identified in *S. Phureja* (Opeña *et al.*, 1979; unpublished). It is possible to transfer the resistance from *S. phureja* to *S. tuberosum* (Gonzales *et al.*, 1973) but the degree of resistance varied with the virulence of the bacterial race.



Fig. 3. A potato plant showing symptoms of bacterial wilt infection.

Robinson (1968) provided evidence of the existence of two resistance forms: race-specific or vertical resistance and non-race specific or field resistance. Some clones had both types of resistance. As with late blight, vertical resistant genotypes showed signs of instability vis-a-vis the pathogen.

4.10 Resistance to virus diseases

Resistance to virus diseases in potato that are important from the breeder's standpoint falls under three categories: resistance to infection, hypersensitivity, and extreme resistance. Another form of reaction (termed "tolerance") to viruses in which the variety is less sensitive and shows only mild symptoms with slight or no yield reduction is also known. Breeding for virus tolerance however is not preferred.

Resistance to infection denotes the difficulty with which a variety becomes infected when exposed to the virus. Hypersensitivity implies extreme sensitive reaction that the virus is localized at the site of infection and no systemic infection occurs (Murphy, 1936). Extreme resistance is equivalent to immunity. This form of resistance was first identified by Schultz and Raleigh (1933) in a seedling that was resistant to PVX even after graft-inoculation.

4.10.1 Potato leafroll virus (PLRV)

As the name implies, the virus elicits upward rolling or cupping of potato leaves (Fig. 4). Not much is known about the genetics of PLRV resistance but many breeders suggest that it is likely polygenic. Resistance can be increased by intercrossing resistant types but is decreased when crossed with susceptibles. Sources of resistance have been identified in *S. tuberosum*, *S. demissum*, *S. andigena*, *S. acaule*, *S. stoloniferum* and *S. chacoense* (see also Table 1).



Fig.4. A potato plant infected with PLRV. Note upward cupping of leaflets.

4.10.2 Potato virus X (PVX)

High levels of resistance (hypersensitivity and extreme resistance) to PVX (see Fig. 5) are known. Resistance to infection is also available in some commercial cultivars and very likely polygenically conntrolled.

Hypersensitivity is conditioned by a single dominant gene inherited in tetrasomic fashion (Cockerham, 1943). Strain groups of PVX have been differentiated (Cockerham, 1955) by using varieties carrying no resistance (genotype $n_x n_b$), either one of the two resistance genes ($N_x n_b$ or $n_x N_b$) and both ($N_x N_b$). Hypersensitivity was tested by graft inoculation which usually leads to a top necrosis reaction, a more reliable criterion than local lesion. Table 4 shows the interrelationship between the genes for hypersensitivity and strain groups of PVX. Hypersensitivity to PVX and PVX^B is determined by genes N_x and N_b, respectively. PVX^B is a strain of PVX.



Fig. 5. Common mosaic symptoms on potato leaves caused by PVX.

Table 4. Interrelationship of genes for hypersensitivity and strain groups of PVX (after Cockerham, 1955).

Variety	Genotype	Strain Group[a]			
		1	2	3	4
Arran Banner	$n_x n_b$	S	S	S	S
Epicure	$N_x n_b$	R	S	R	S
Arran Victory	$n_x N_b$	R	R	S	S
Craigs Defiance	$N_x N_b$	R	R	R	S

[a]R = hypersensitive; S = susceptible

Of the four strain groups, Group 3 is the most common and economically, the most important. Common strains of PVX belong to this group. Group 4 strain which is the most dangerous has not been found in commercial potatoes and only one strain has been described in the literature so far (Wiersema, 1972). Identification of reaction to Group 4 is usually done by grafting PVX^{B} -infected scions onto N_xN_b cultivars (Cockerham and Davidson, 1963; Rozendaal, 1966). Presumably, PVX^{B} mutates easily into a Group 4 type to infect all known N_xN_b varieties. Strains of Group 3 can also be obtained by grafting PVX^{B} scions onto n_xN_b varieties. PVX^{B} strain belongs to Group 2.

The drawback of hypersensitivity to PVX is that resistance is race-specific. Lessons from other crop diseases (rusts of cereals or late blight of potato) suggest that this type of resistance is unstable. Varieties carrying gene N_x have been grown for more than a century, however, without resistance-breaking strains arising (Wiersema, 1972). Hypersensitivity still seems to be a valuable form of resistance in potato breeding.

Immunity to PVX was first discovered by Schultz and Raleigh (1933) in the seedling USDA 41956 with a Chilean variety in its background. CPC 1673, an *S. andigena* clone in the Commonwealth Potato Collection (England) also showed extreme resistance. Another source is the wild species, *S. acaule*.

A single dominant gene, Xi, governs extreme resistance to PVX in *S. acaule* (Cockerham, 1958; Ross, 1961). The alleles Xn and x gave hypersensitive and susceptible reaction, respectively. Xi is dominant over Xn. The genetic relationship between Xi and Xn suggests that extreme resistance (due to Xi) is an extreme form of hypersensitivity.

4.10.3 Potato viruses A (PVA), Y (PVY) and S (PVS)

Resistance to infection by these viruses is known and most likely polygenic in inheritance. Hypersensitivity to PVA, PVY and PVS and immunity to PVA and PVY have also been identified. Fig. 6 shows the typical symptoms caused by PVY.

Single dominant genes Na and Nc condition hypersensitive reaction to PVA and PVY^{C}, respectively (Cockerham, 1943). Gene Ns, identified from a Bolivian Andigena clone (PI 258907) determines hypersensitivity to PVS (Baerecke, 1967).

The gene Na, conditioning hypersensitivity to all strains of PVA is closely linked to N_x (hypersensitivity to PVX). Most cultivated varieties, e.g. Bintje, Eersteling, Grata, Irish Cobbler, Katahdin, etc., carrying gene N_x are also hypersensitive to PVA (Wiersema, 1972). The close linkage between Na and N_x is very convenient from a breeding standpoint.

The gene Nc which conditions hypersensitivity to PVY^{C}, an unimportant strain of PVY, does not confer resistance to strains PVY^{O} and PVY^{N}. No genes for hypersensitivity to PVY^{O} and PVY^{N} strains are available (Wiersema, 1972).

Immunity to PVA and PVY is controlled by a single dominant gene and has been identified in *S. stoloniferum* (Cockerham, 1955; Ross, 1961). Like the immunity to PVX, extreme resistance to PVY is governed by three alleles. The gene for immunity to PVY and PVA only needs to be combined with gene Xi (extreme reaction to PVX) to obtain complete protection against all strains of PVA, PVY, and PVX. Therefore, breeders prefer breeding for immunity to all three viruses to breeding for hypersensity because only two genes are needed to be combined into a new clone.



Fig. 6. Typical symptoms caused by PVY.

5. Varietal Improvement Schemes

Potato breeding follows the same fundamental principle as in other crops—it involves selection of the most desirable genotype for a specific purpose. The raw materials (or variability) for selection could arise from natural or artificially induced variations. Introduction of exotic germplasm and spontaneous mutations (including naturally occuring gross chromosomal changes, e.g. shifts in ploidy level) fall under natural variations.

Sexual hybridization between potato clones is the traditional method of generating artificially induced variations. Induction of mutation, chromosomal aberrations, and shifts in ploidy level also create phenotypic and genotypic changes that breeders could work on although, as already stated, their overall contribution to varietal improvement of potato has been limited. Nevertheless, they are sources of variations that may be utilized whenever desirable variants arise because vegetative propagation insures that such variants remain true-to-type. Genetic changes could also occur in tissue-culture propagation of potato and as such, may add to exploitable variation. A sophisticated approach currently under development is the use of protoplast fusion to generate new variation. Variations among plantlets derived from pure protoplast cultures are also being explored. However, it may take some time before such method can be included among the plant breeder's arsenal of routine breeding techniques if ever the approach proves feasible.

This section is divided into two broad topics. First, emphasis is placed on traditional breeding techniques including introduction, hybridization and selection. Subtopics under each section are provided to elucidate relevant subjects. Second, non-traditional or unconventional breeding methods are presented to provide a broad view of the genetic

improvement efforts in an important food crop like potato. Topics such as breeding possibilities at the dihaploid level, mutation breeding, tissue culture and protoplast fusion techniques, and the development of TPS (true potato seed) technology are included. While it may be argued that most potato breeding is technology rather than science (Howard, 1970), it does not mean that plant breeders can ignore advances in basic scientific knowledge which may be important in facilitating their breeding efforts and/or understanding better the rationale of the approaches they have undertaken.

5.1 Conventional breeding methods

Germplasm introduction, screening of genetic materials for major characters of importance, release and/or utilization of elite clones in a program of hybridization and selection, are collectively still the "bread and butter" of potato breeding programs throughout the world. Although the levels of sophistication and the magnitude of efforts may vary, much of potato breeding is, and will remain for some time to come, crossing two clones which complement each other in terms of important traits in order to select from the offsprings a new clone which combines the good qualities of both parents (Howard, 1978).

Some programs, especially those involved in breeding for special traits like processing quality and resistance to environmental stress such as high temperatures, have utilized population breeding methods because of the relative genetic complexity and/or low gene frequency of desirable alleles of the traits being dealt with. Backcross method has also been widely used in breeding for disease resistance especially when genetic control is fairly simple and the source of resistance is an unadapted clone.

5.1.1 Germplasm introduction

Potato is indigenous to the Andean regions of South America (particularly Peru and Bolivia) and was undoubtedly domesticated there. It is there where the greatest amount of genetic diversity occurs. Many wild species can also be found in Mexico and Central America but these never seem to have been taken into cultivation and the apparently indigenous forms of *S. tuberosum* there all seem to have come from South America, probably in the early post-conquest days (Hawkes, 1978).

The history of potato development as a crop in Europe, North America and the rest of the world traces back to introductions from South America, first into Spain in 1570 and secondly into England a little later. There has been some controversy as to what region of South America the original introductions into Europe came from and whether subspecies *tuberosum* from Chile or subspecies *andigena* from the Andes was first introduced (Juzepczuk and Bukasov, 1929; Salaman, 1964; Salaman and Hawkes, 1949; Salaman, 1954; Hawkes, 1967). Regardless of the disagreements, the movement of potato and its subsequent transformation into a major food crop constitute a classic example of the importance of plant introduction to agricultural development.

Introduction of diverse genetic materials continues to be an important component of varietal development in potato. This must be so especially when the limited genetic variability from which present day Tuberosum cultivars have been bred is considered (Simmonds, 1962). The original introductions from South America were likely few and further decimation of this germplasm by the late blight epidemic of the 1840's must have reduced the store of variability even further. The difficulty of replacing old potato cultivars with new varieties coming from intra-Tuberosum crosses partly attests to the limitations imposed by narrow variability.

Already, there are indications that infusion of diverse materials into the Tuberosum gene pool leads to significant heterosis for yield. Glendinning (1969) found a 13% yield improvement of Andigena x Tuberosum crosses over Tuberosum x Tuberosum crosses, the two progeny groups having similar mean maturities. Other workers (Toxopeus, 1952; Rothacker, 1962; Cubillos and Plaisted, 1976; Tarn and Tai, 1977) provided supporting evidences to underscore the importance of genetic diversity in further improvement of potato. The need to exploit the existing variability has been eloquently described in an assay on this topic by Bennett (1965).

Every breeding outfit must have its own store of variability from which the plant breeder could readily draw materials essential to his program. In countries where potato ranks as a major food crop, the task of collection, maintaining, cataloguing, and distribution of introductions has become a specialized service rendered by a national potato introduction station or agency. Examples of these national collection centers are: USDA potato collection in Sturgeon Bay, Wisconsin; the Dutch potato collection at Wageningen; and the Commonwealth Potato Collection in Scotland. Plant breeders in these countries no longer need to worry about maintaining their own individual collection, although to a limited extent, each breeder invariably keeps a core of elite clones that are considered the mainstay of a specific program. These clones are however usually duplicates of those in the national collection center and are only kept for easier access.

The largest single collection of potato species, cultivated and wild, is held at the International Potato Center (CIP) in Peru. Being at the center of origin and diversity, the CIP collection is considerably augmented year after year. More importantly, valuable genetic materials that would otherwise be irretrievably lost in the aftermath of further agricultural technology and population encroachments into previously undisturbed areas continue to be preserved. CIP scientists have been maintaining, cataloguing and evaluating this collection and distributing important materials therefrom world-wide. The development of tissue-culture technique (Roca et al, 1979) has not only facilitated the transfer of germplasm from CIP but also effectively removed the danger of introducing certain pathogens and pests unknown in countries where potato is not a native crop.

Developing countries, especially in tropical areas where potato is still a minor crop, either do not yet have the capability nor likely the urgent need to maintain collections in the manner and scale that is being done in other countries (or institutions) such as those mentioned above. Much of the effort heretofore had been restricted to variety introductions from temperate countries for testing under local conditions and eventually, release of outstanding clones for commercial production. There is however a growing interest in some of the developing countries to embark on their own breeding program for more extensive crop development (see Section 1). In a few cases, hybridization and selection on a limited scale have been in place for some time now. However, the genetic base in these breeding programs is almost always restricted to introduced Tuberosum cultivars which, as a gene pool by itself, is already narrow. Therefore, the chance of a significantly improved clone arising from such programs is remote even if one considers realistically that the standard of varietal acceptance in these countries is conceivably less rigorous.

Without going to the extent of establishing a germplasm center, it is easily possible for national potato programs to infuse genetic diversity into their breeding activities. A wide range of materials is generally readily available in true seed or clonal forms from large collection centers such as at CIP, USDA, and others. As already mentioned, the transfer of

tissue-cultured materials and other pathogen-tested clones should appreciably ease the fears of introducing, along with the clones, dangerous pests and diseases.

A pervasive willingness to share genetic materials exists among the major germplasm repositories. However, national programs should reciprocally develop an effective system to receive and multiply the introduced materials prior to their evaluation and utilization. Much of the difficulty lies in the transfer of tubers which, being in an active metabolic state, do not last very long in transit. Some national programs often strictly adhere to the principles of plant quarantine even without the basic facilities to keep introductions in viable state and test them accordingly. As a result, tuber introductions are almost always spoiled before they are received by research stations or other requesting agencies.

Plant quarantine is unquestionably essential to prevent the introduction of harmful pests and diseases. Nonetheless, a certain degree of flexibility may be maintained without unduly sacrificing the principles of disease and pest isolation especially where introductions come in tissue-culture form or guaranteed to be pathogen-free. Without this flexibility or better yet, an organized system for receiving and utilizing introductions, much time, money and effort spent by germplasm donors will continue to be unfairly wasted.

5.1.2 Evaluation of introductions

Soon after sufficient quantity of the introduced materials has been multiplied, these are evaluated according to the purpose for which materials were obtained. These tests, or series of tests as the case may be, could involve evaluation for yield and other horticultural characters, resistance to pests and diseases, certain quality attributes, or other traits that particular program considers essential in a specific geographical location.

In almost all cases, successful evaluation generally requires interdisciplinary cooperation between plant breeders, horticulturists, plant pathologists, entomologists, etc. The appropriate combination of discipline obviously depends upon the character under evaluation. Even in certain disciplines, area specialization necessitates a choice of the proper individual to include in a team of cooperators. For example, a fungal pathologist should be the specific person working with breeders in screening for resistance to late blight while a virologist is more appropriate for viral disease. Because of the diversity of disease and pest problems in potato, a team of scientists should ideally encompass most of the major disciplines and their specialized areas.

It has been mentioned that the evaluation of introductions (especially commercial cultivars) in developing countries without any ongoing breeding programs has been limited to determining their potential for commercial production. In most cases, a variety testing program would include evaluation for yield and other important horticultural attributes, relative resistance to diseases, and observations on tuber appearances such as shape, size and flesh color, where these traits contribute to acceptability standards. For example, round oval tuber with yellow flesh is preferred over other types in Indonesia. The series of tests that an introduction ideally should go through is depicted in Fig. 7.

It is important to note that the good state of health of introductions, especially with regards to virus problems, should be maintained during the multiplication process. Otherwise, the evaluation trials particularly relating to general yield performance will be biased against virus-infected clones. Where there is no scheme for insuring healthy and rapid clonal propagation, the least that can be done is to practise positive mass selection of healthy clones to produce reasonably healthy tuber samples for trials.

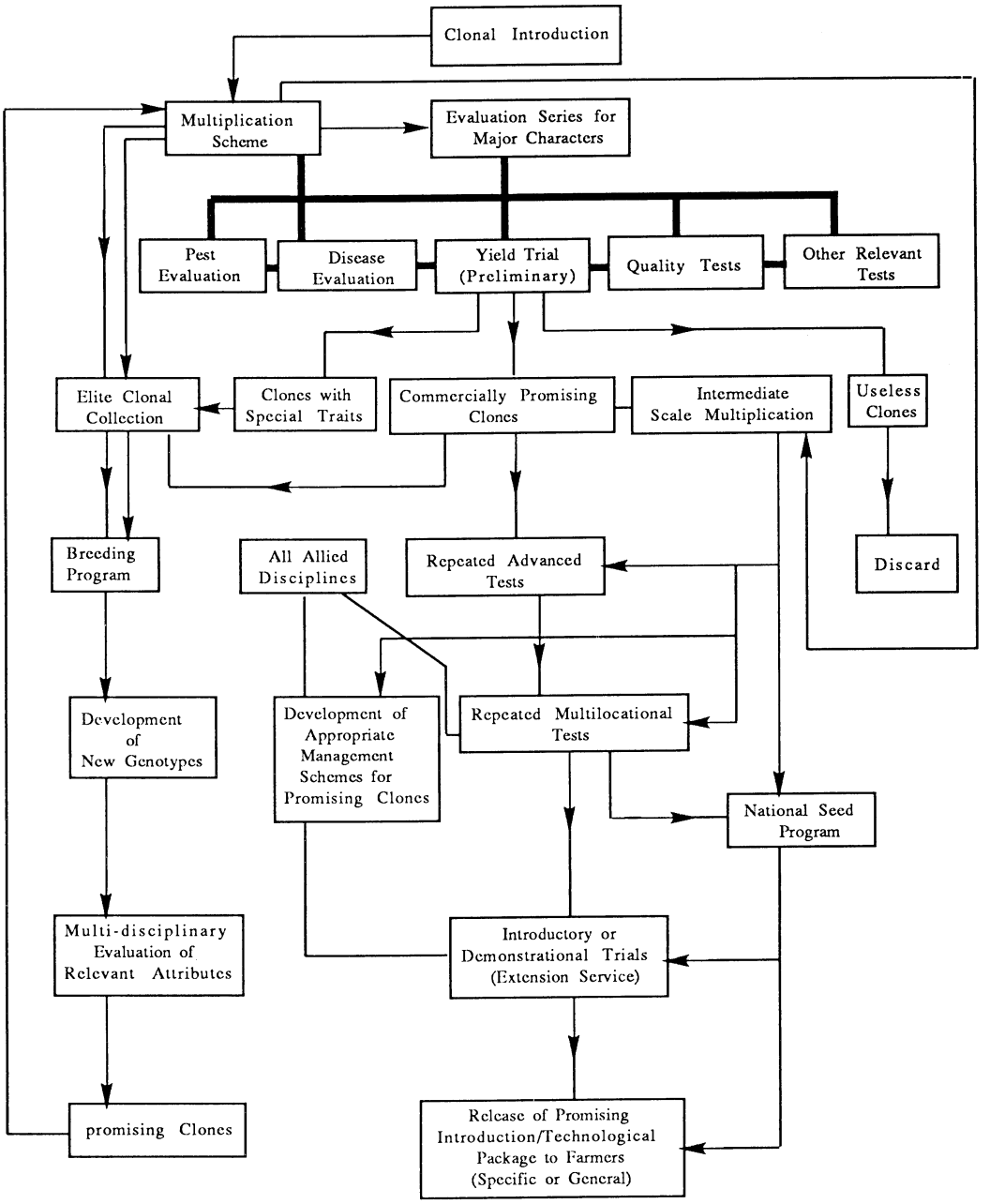


Fig. 7. An idealized flowchart for potato germplasm introduction, evaluation and utilization in a developing country with an on-going breeding program(solid line with arrow at the end = flow of materials; solid line with arrow in the middle = flow of information).

5.1.3 Utilization of introductions

Practically speaking, introductions serve no purpose unless they find their use directly into the agricultural production sector or contribute useful genes they may carry in the development of improved cultivars. In countries without breeding programs and which import only commercial varieties for testing, unadapted clones simply become obscure and eventually lost. Outstanding clones, however, are almost always released as commercial cultivars especially when seed are readily available from exporting nations and further importation is considered economically feasible.

Where a breeding program and a concomitant collection exist, clones that are not outstanding commercially, but carrying special trait(s) such as resistance to important diseases and pests, outstanding quality, etc., should revert back to the germplasm assembly for maintenance and use in breeding activities. It is tempting to imply that ideally all introductions should be maintained by all means but consideration of available resources and technology in developing countries will promptly show that keeping only the elite clones is a far more rational approach than non-selective propagation of all. The latter could be left to large germplasm collection centers, national, regional, or international in scope.

The International Potato Center has, in recent years, developed alternative regional gene banks such as at Colombia and the Philippines. Once fully operational, these regional gene banks could very well serve the needs of national programs within each region and should further justify a program of only selective germplasm maintenance for a specific country.

A diagram of germplasm flow in Fig. 7 illustrates an idealized stepwise movement of clonal introductions from the time they are received until they are utilized. An assumption is made that the introductions are potentially useful commercial cultivars and the scenario is a developing country with an ongoing breeding, elite clonal maintenance and seed production program.

5.1.4. Hybridization and selection

In a catch-all sense, hybridization entails a directed generation of variability for the purpose of choosing (selecting) an improved type. In potato, such variation is immediately released upon crossing a pair of clones because of the inherent heterozygosity of all cultivars. Potato breeding, therefore, appears at first glance to be a simple matter of selecting the most desirable seedlings in the "F_1" generation and asexually mass-propagating the selections thereafter. However, as already described in Section 3, the consequences of vegetative propagation, genetic status, and the tetraploid nature of potato, easily offset the above advantage. Most of the economically important characters in potato are also genetically complex and easily influenced by environmental vagaries that it is virtually impossible to select for them in the early clonal generations.

In this section, the important technical aspects of hybridization are discussed initally. Thereafter, methods of breeding and selection are given. Finally, breeding for specific traits, especially those considered of prime importance in the tropical countries, are provided.

5.1.4.1. Establishment of priorities for breeding

Potato is a prime example of a major food crop with multitude of problems. Depending upon the country, these problems could broadly range from aspects of general performance and adaptation, pests and diseases, and quality attributes for a wide array of usage. Considering that each of these problem categories further subdivides into a number of

specific problems, potato breeders are easily confronted with a host of possible breeding objectives.

Because of this multiplicity of problems, the chance of breeding a successful potato variety is small. Plaisted (1966) estimated that on the average, a breeder can expect to produce a significant variety only once in 15 to 20 years. Wiersema (1961) calculated that only one out of 150,000 seedlings reaches the "List of Varieties" in Holland.

In an overview on this apparent dilemma, Simmonds (1969) very clearly stated that realism is the first important requirement in framing a potato breeding program. Using an example, he arrived at the clearcut conclusion that, breeders must either select for fewer characters or select less intensively.

Comparing the two alternatives, it is far better to review the possible breeding goals under certain conditions and synthesize a set of simplified priorities rather than have a broad range of objectives which is difficult to satisfy *en toto*. Moreover, exercising less stringent selection to encompass multiple objectives effectively reduces to breeding for fewer characters unless a good selection index (Tai, 1977) can be easily found, but even assuming so, it is doubtful whether it can be adopted as a practical breeding tool (Simmonds, 1969).

Establishing a set of simplified breeding objectives may entail a number of coordinated activities. First, a survey of commercially grown varieties should provide the breeders with information as to which are the most popularly grown cultivars, their assets and liabilities. Where a well-organized extension service exists, their assistance in identifying the most pressing production problems should be availed of. Oftentimes, experimentation may be necessary to decide which problems are the most critical. For example, studies on extent of yield reduction, intensity of distribution, etc. may help in prioritizing the diseases and/or pests problems to solve through breeding. Plant breeders and cooperating scientists should neither neglect the importance of contact with farmers and observations of their commercial fields for aid in decision-making. Before formulating a breeding program, all possible sources of information should be examined to insure that priorities are clearcut and relevant.

In developing countries, potato breeders can seek comfort in the fact that the requirements for any new variety are less rigid than where potato is commercially a highly developed crop. The limited and unsophisticated utilization of potato in developing countries practically minimizes breeding for high quality both for processing and immediate consumption. Statistics on potato utilization in developing countries show that processing is not an important component (Horton, 1978). However, times do change and breeders should always be prepared to respond to contemporary market demands. At the present time, it may be safely presumed that potato breeders in developing countries should concern themselves mostly with breeding for high yield and adaptability (especially to short daylength and relatively high temperatures), resistance to major pests and diseases, and perhaps, to some extent, a few important quality attributes. Some countries have preferences for example for particular tuber shapes, flesh and skin colors, and size. Most of these traits are, however, easier to breed for than cooking and processing quality components in view of their relatively simple genetic control (see Section 4).

With respect to disease and pest resistance as breeding objectives, a certain amount of realism will again be needed. A survey of production areas will invariably reveal a variety of pests and diseases but not all likely deserve the breeder's attention. In some cases, chemical control of certain diseases or pests or some other means of control may prove to be highly economical already. A good seeed program can practically eliminate the need to breed for virus resistance, and incorporation of stem-cutting techniques in the scheme is effective in controlling blackleg (*Erwinia carotovora* var *atroseptica*) and possibly other tuber-borne diseases (Hardie, 1971 ; Calvert, 1973). Naturally, it can be strongly argued with good reason that the use of resistant varieties is still the cheapest method of controlling pests and diseases. However, a successful plant breeder is always a practical one and considering the many problems he has to solve, one less objective contributes to his chances everytime.

5.1.4.2. Choice of parental breeding stocks

The survey of locally grown cultivars can provide breeders with good benchmark information to help him identify potential parent clones for the breeding program. Oftentimes, a situation exists where some cultivars are deficient only in a few important attributes to become a highly successful variety. If these are available, the problem becomes one of finding among other clones those traits which adequately complement the outstanding characteristics of the other parents. If not available, efforts should be made to secure the valuable germplasm from other sources.

Sometimes, the desired combination of characters may already be in an established cultivar elsewhere and initiating a breeding program may, in the long run, be more costly than importing that cultivar. The value of germplasm introduction on this regard is very obvious. The testing program for introduced varieties should not lose sight of the general breeding goals to insure that potential solutions are properly adopted.

In general, four groups of parents are available to potato breeders. These are varieties of Group Tuberosum, Group Andigena, cultivated diploids, and wild species. Tuberosum cultivars are adapted to long days typical of summers in temperate countries. Under the short days of the tropics, these cultivars tend to mature earlier and therefore, are comparatively less productive. Nevertheless, most of the potato varieties grown in the tropical countries (except in South America where potato is indigenous) belong to Group Tuberosum.

When the characters of interest to potato breeders are not available in the Tuberosum gene pool, the next best source is Group Andigena. There is undoubtedly a substantial amount of variability present in the Andigena gene pool (Plaisted, 1977). Valuable genes for potato breeding that are known to be present in Group Andigena are: field resistance to late blight ; immunity to PVY and PVX; resistance to PVS, common scab, wart and Verticillium wilt; and resistance to aphid species *Myzus persicae* and *Macrosiphum euphorbiae* (see Table 1). The gene pool itself had incontrovertibly given rise to the present day Tuberosum gene pool when small samples of short-day adapted Andigena potatoes introduced into Europe were subsequently selected for long day adaptation there. Simmonds (1966) and Plaisted (1972) have attempted to repeat what undoubtedly was a slow adaptation process by practising intense selection for key Tuberosum characters on genetically broad Andigena populations. All indications are that the morpho-physiological changes which characterized the evolution of Tuberosum from Andigena gene pool are indeed repeatable.

The cultivated diploids are likewise a highly variable group with a tremendous reserve of genetic potential which has remain largely untapped. Useful genes in this group range from : resistance to virus diseases such as PVA, PVX, PVY and leafroll; resistance to late

blight, ring rot, bacterial wilt and Verticillium wilt; resistance to insects such as flea beetle and aphids; nematode resistance; frost resistance; and high dry matter content (see Table 1). There appears to be no difficulty in crossing cultivated diploids and tetraploids. Marks (1966) observed that the results of such crosses are often tetraploid, not the expected triploid offspring, primarily due to the appreciable frequency and normal functioning of unreduced gametes in the diploid parent.

A gene pool of last resort is the wild species. Potato breeders have used wild species in hybridization programs only when the genes sought after are not available in cultivated groups or even if so, intensity or level of gene effects such as those conditioning resistance to diseases or pests is low. The conservatism in the use of wild species for breeding purposes is understandable when one considers the length of time it takes to transfer the useful genes into the genetic background of cultivated potato. Undesirable characters from the wild often accompany such transfer and occasionally, these traits are difficult to eliminate especially if they are closely linked to the gene(s) of interest to the breeder. A prime example of valuable genes successfully transferred from the wild species into *S. tuberosum* are the R-genes for resistance to late blight from *S. demissum*. Other potentially useful genes from wild species are : resistance to golden nematode in *S. vernii, S. oplocense, S. spegazinii, S. sparsipilum, S. boliviense, S. brevicaule,* and *S. megistacrolobum* (Ellenby, 1952; Ross and Huijsman, 1969; Deshmukh and Weischer, 1970); resistance to aphids in *S. polyadenium, S. tarijense, S. berthaultii*, and other wild species (Gibson, 1971; Radcliffe and Lauer, 1971); resistance to Colorado beetle in *S. chacoense*; extreme resistance to all strains of PVY in *S. stoloniferum* (Cockerham, 1970); resistance to PLRV in *S. demissum, S. acaule, S. chacoense* and *S. stoloniferum* (Wiersema, 1972); and many more (see Table 1).

As cited in Section 2, most wild and cultivated diploid potato species can cross easily and the resulting F_1's are fertile and vigorous. The absence of strong breeding barriers between most potato species is a tremendous advantage to plant breeders because it considerably widens the range of genetic variabliity that they can utilize.

5.1.4.3. Breeding methods

Traditionally, the systems of breeding used in potato have been by pedigree method or in some cases, by backcross method. Population breeding methods, such as recurrent selection, have gained acceptance among breeders involved in improving clones for characters conditioned by polygenes, e.g., yield, dry matter content, and other important traits, especially those contributing to processing qualities (plaisted, 1966).

5.1.4.3.1. Pedigree breeding

As already mentioned, much of potato breeding has been and will perhaps remain for some time, crossing a pair of clones which complement each other in desirable attributes in order to select a new clone possessing the good qualities of both parents. In general, a series of crosses is usually necessary to accumulate a number of good traits into a single clone. This is the so-called pedigree breeding method.

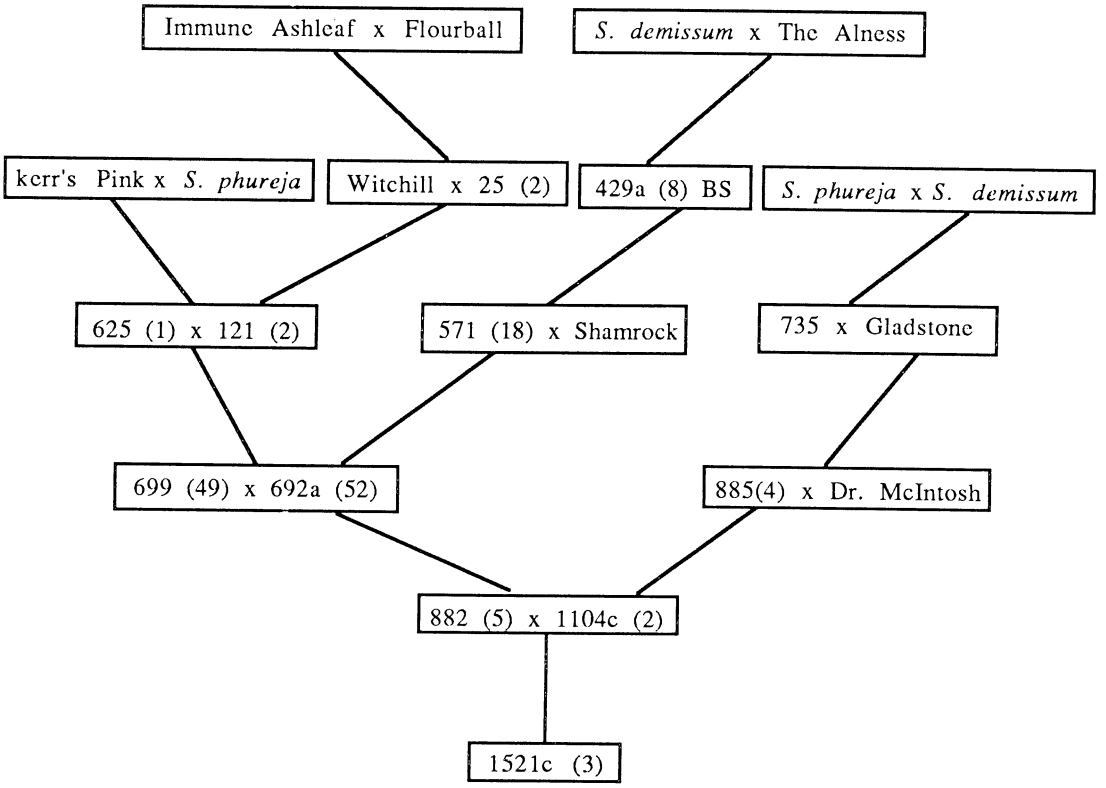


Fig. 8. Pedigree of Roslin Ebrur (after Black, 1972).

Pedigree method works very well when the characters to be accumulated in a new clone are simply inherited and conditioned by dominant genes. This is expected since the desirable genotypes appear in high frequencies and can be selected right away among the immediate hybrid progenies. Assuming that only two dominant genes are to be combined and chromosome segregation is random, the proportion of desirable genotypes can range from 25—100% depending upon the genetic configuration of the parental clones (Table 5). The least proportion (25%) arises only from simplex x simplex mating but even that frequency is already sufficiently large considering that thousands of progenies, not hundreds, are normally handled in a potato breeding program. A good example of variety produced by pedigree method is Roslin Eburu, a variety released in Kenya which occupies most of the acreage in East Africa (Black, 1972). Although its field resistance to blight is only moderate, the degree of resistance it possesses together with its adaptation to short-day conditions and its cropping propensity has established it over a wide area. The pedigree record of Roslin Eburu is shown in Fig. 8. Note the series of crosses made before arriving at the final clone.

With traits that are controlled largely by recessive genes, the proportion of desirable genotypes among hybrid progenies is drastically reduced and can only be recovered (assuming only random chromosome segregation) when both parents are at least duplex for all the genetic factors in question. Even so, the expected number of progenies homozygous for the recessive alleles (assuming that only two genes are to be combined) is only one in

1,296 seedlings. This proportion is greatly incremented as the dosage of the recessive alleles increase in each parent. For example, using the two - gene model again, this proportion is now 1/8 if one of the parent clones is already homozygous recessive (nulliplex relative to the dominant gene) for one of two genes and has the other in triple dose (simplex for the dominant gene) while the other parent has both recessive genes in triple dose, i.e., the genetic cross configuration is Aaaabbbb x AaaaBbbb.

Simplified genetic situations as the above naturally are rarely, if ever, encountered in actual potato breeding partly because breeders are normally concerned with combining more than two characters into a single clone, even in an idealized case where the major traits sought after are simply inherited. Moreover, random chromatid segregation is also known to exist in *S. tubersosum*. This phenomenon will only slightly alter the genetic ratios but it will enable triplex parents (AAAa) to produce a low frequency of nulliplex (aa) gametes or conversely, simplex parents (Aaaa) to produce duplex gametes (AA). Catcheside (1959) also pointed out that production and functioning of aneuploid gametes could give results similar to those expected from chromatid segregation. This appears to have some cytological basis as normal meiosis in *S. tuberosum* usually shows, in addition to quadrivalents and bivalents, also univalents and trivalents (Wangenheim, 1955; Swaminathan, 1954a; 1954b). Univalents and trivalents could lead to the formation of aneuploid gametes.

Table 5. Theoretical frequency of desirable genotypes, i.e. progenies which combine the dominant genes from complementary parents, in the immediate hybrid population in all possible mating schemes[a].

Type of of mating	Hypothetical parent genotype	Expected frequency of desired genotypes
		(%)
simplex x simplex	Aaaabbbb x aaaaBbbb	25
duplex x duplex	AAaabbbb x aaaaBBbb	70
triplex x triplex	AAAabbbb x aaaaBBBb	100
quadruplex x quadruplex	AAAAbbbb x aaaaBBBB	100
simplex x duplex	Aaaabbbb x aaaaBBbb	42
simplex x triplex	Aaaabbbb x aaaaBBBb	50
simplex x quadruplex	Aaaabbbb x aaaaBBBB	50
duplex x triplex	AAaabbbb x aaaaBBBb	83
duplex x quadruplex	AAaabbbb x aaaaBBBB	83
triplex x quadruplex	AAAabbbb x aaaaBBBB	100

[a]Using a two-gene model and assuming random chromosome segregation.

5.1.4.3.2. Backcross breeding

When one of the parent clones in a cross is commercially an unadapted type but carries an important trait lacking in the other parent (usually a valuable commercial variety), breeders resort to the system of backcrossing. A good example is the transfer of resistance to golden nematode (*Globodera rostochiensis*) from Group Andigena to *S. tuberosum* cultivars adapted to the northern belt of the United States (Plaisted, 1966). Another is the incorporation of major R - gene resistance to late blight from the wild hexaploid species, *S. demissum*, to tetraploid *S. tuberosum* (Marks, 1960).

As in other crop plants, the backcross method in potato is greatly facilitated if the character under transfer is simply inherited and conditioned by a dominant gene. In the simplest case of incorporating a monogenic dominant gene, segregation occurs in the immediate F_1 if the donor parent is simplex (Aaaa) or duplex (AAaa). Naturally, the recurrent parent (or the recipient) is nulliplex (aaaa) for the gene. The proportions of hybrid progenies with the desired dominant gene are 50% and 83%, for simplex and duplex donors, respectively. Thus immediate backcrossing to the recurrent parent is possible assuming that a good selection regime (especially when dealing with pest or disease resistance) is available to pick out the progenies carrying the dominant gene. With triplex (AAAa) or quadruplex (AAAA) donors, there is no observable segregation in the F_1 and backcrossing can proceed more normally. Regardless of the genetic status of the donor, however, every backcross generation thereafter will exhibit segregation for the dominant gene under transfer. Therefore, the appropriate backcross derivatives to use in further backcrossing must be continually selected.

The backcross procedure is far more complicated and slower when the desirable gene from the donor parent is inherited in a recessive fashion. In the single gene model where the recurrent parent does not carry the recessive allele, i.e., AAAA, the dominant allele masks the desirable recessive allele in every generation. Thus, it is necessary for the breeder either to self or intercross progenies every time in order to select the clone which expresses the desired trait for use in further backcrosses. Alternatively, the breeder can dispense with progeny tests and continuously backcross using a representative sample of progenies in every backcross. Bulk-pollen hybridization can facilitate this procedure. However, though faster and possibly less time consuming, there is always the danger that the gene under transfer could be inadvertently lost in the process. This problem could become magnified especially when progenies have a wide range of flowering time that some unavoidably cannot contribute to the next generation. A possible solution might be to regularly intersperse the progeny test every 2 or 3 backcrosses as a spot check for the presence or absence of the desired gene.

A situation may be visualized whereby the intended recurrent parent is already heterozygous for the desired recessive gene. In such special case, the pedigree method is more suitable than the time-consuming, tedious backcross system assuming that another heterozygous parent is available so as to uncover the homozygous recessives either in the immediate hybrid progenies or from F_1 intercrosses, as the case may be. Selfing heterozygous clones (especially those with two or three doses of the recessive allele) should, of course, reveal the homozygous recessives immediately. However, potato is an outbreeder and is known to exhibit inbreeding depression upon selfing (Krantz, 1946). Nevertheless, such homozygous recessives from a selfing program may be used directly as parents.

The cultivated potato is highly heterozygous and therefore, the genetic background of the recurrent clone is virtually impossible to recover. Nonetheless, further selection among the F_1's and backcross derivatives carrying the desired gene under transfer, for general traits more or less typical or progressively near the recurrent parent, should accelerate the reconstitution of a desirable genetic milieu. This is especially useful when the donor parent is a highly unadapted type, e.g. wild species. Selection of such derivatives is considered equivalent to saving one or two backcrosses (Briggs and Knowles, 1967).

The number of backcrosses to make depends upon a particular situation. Generally, it can range from three to ten. As already noted, the potato breeder cannot fully reconstitute the exact genetic background of the recipient clone. Therefore, as soon as the frequency of commercially adapted types carrying the desired gene(s) being transferred is already

significant in a specific backcross generation, the derivatives are often subsequently handled by pedigree method to select the best clones. Obviously, the number of backcrosses required to reach such a stage is dependent upon the nature of the donor parent—wild species as gene donors will require more, for example, than say donors from Group Andigena, when backcrossed to *S. tuberosum* cultivars.

Progeny testing of derivatives from the last intended backcross generation cannot be dispensed with when the gene under transfer is recessive. Pedigree handling of the homozygous recessives follows thereafter. With a dominant gene, this procedure is not necessary as long as the last backcross derivatives are effectively selected.

5.1.4.3.3. Population breeding

Many economically important characters in crop plants exhibit polygenic inheritance. In contrast with the classical Mendelian genes, i.e., those with large, easily discernible effects, polygenes do not follow clearcut segregation ratios and generally, there is no one to one correspondence between the phenotype and the genotype of an individual. The reasons for these peculiarities are as follows: many genes each with small individual effects control polygenic characters; gene interactions are more often a rule than an exception; and the genotypic expression is highly influenced by environment.

In potato, there too are many important characters under polygenic control, e.g., yield, maturity (under a specific daylength), dry matter, and certainly, most processing quality attributes such as after-cooking darkening, levels of reducing sugars, etc. In breeding for these traits, breeders are often faced with the problem of how to carry out selection in a most effective and efficient manner.

The cultivated potato is a tetraploid which means that a gene is present four times in an individual. Using for simplicity just a two-gene model in which we assume that there only two alleles per locus, that each gene contributes equally to the phenotype, and that dominance, epistasis, and environmental effects are completely absent, only two genotypes (which may be symbolically represented as AAAABBBB and aaaabbbb) in a hybrid population exactly match their phenotypic expressions. Other phenotypic values are already, even in such exceedingly simple model, represented by a range of two to five genotypes. Selection of a particular phenotype therefore will not necessarily indicate its true genotype.

In real situations, the simplifying assumptions of the above model certainly do not hold. Breeders usually can anticipate a preponderance of loci conditioning complex charactes, interaction between loci, unequal contribution of loci to the total phenotype, significant environmental effects and varying dominance levels at different loci. It is thus easy to visualize how the idiosyncracies of polygenes can greatly confound the breeder's dilemma.

Recurrent selection as a population breeding method has received increasing use for improving characters in potato that are under polygenic control (Houghland *et al,* 1961; Plaisted and Peterson, 1963; Stevenson et al, 1954; Mendoza, 1976; Opeña, 1976; Tarn *et al,* 1977). The method is designed to increase the frequency of superior genotypes in breeding stocks. Recurrent selection accomplishes this by increasing the frequency of superior genes in the gene pool and by increasing the chances or genetic recombination to occur.

As the name implies, recurrent selection systems are cyclic in nature. Hull (1952) succinctly defined the method: "Recurrent selection was meant to include reselection generation after generation, with interbreeding of selects to provide for genetic recombination. Thus, selection among isolates, inbred lines, or clones is not recurrent until selects are interbred and a new cycle of selection is initiated". Each cycle requires evaluation

and maintenance of selections, and intercrossing the superior selection (or their self progenies) in all possible combinations and bulking of equal amount of seeds from each cross to initiate the next cycle.

The evaluation of selections in each cycle may be based simply on their phenotypic expressions for character of interest or on progeny test. The first method is called phenotypic recurrent selection. As the value of a selection is assessed from information from a single individual, the method is expected to work well for characters with relatively high heritability. Plaisted and Peterson (1963) reported nonetheless the efficacy of phentypic recurrent selection in improving potato dry matter content, a genetically complex trait. Three cycles of recurrent selection increased the dry matter 20% above that of cv. Katahdin and 2 cycles increased it 8% above the average of Delus, Green Mountain, Saco, Houma and Merrimack, cultivars which were chosen as parental clones because of their high specific gravity. Although their method falls under phenotypic recurrent selection, it must be pointed out, however, that their selection of clones for each intercrossing cycle was based on three-year tests. Here again, vegetative propagation enables multiplication of selections without loss of genetic identity and clearly provides potato breeders with a unique advantage not normally available to seed crop breeders.

As an accessory tool in recurrent selection, progeny tests aid breeders in assessing the genetic worth of selection as parent stocks. Genetically variable testers give rise to recurrent selection for general combining ability. When the tester is genetically narrow, recurrent selection is for specific combining ability.

The average performance of a potato clone as a parent in a range of crosses is referred to as the general combining ability of that clone. This information is particularly valuable in the sense that it measures the breeding value or the ability of a clone to pass on its good characteristics to its offsprings. Some clones may, by themselves, be outstanding but be poor parental stocks. Some studies have clearly shown the existence of differences in combining ability among clones for yield, specific gravity, and tuber appearance (Sanford, 1961; Plaisted *et al,* 1962). Plaisted (1966) cited how progeny tests have been used to identify clones which on the average produced progenies less apt to turn dark after cooking than most other clones.

Using mainly good combining clones in the hybridization program should considerably help breeders to further refine the breeding activities. Progeny tests, in other words, provide breeders with a rational method of choosing parents.

5.1.4.4 Flowering induction and enhancing success of pollinations

The development of flowers and fruits (technically called "berries") in potato is related to source-sink balance in the plant. Without the essential nourishment, flower buds abort or even if full grown flowers have been produced and pollinated by a known pollen-fertile clone, flowers tend to drop. In some cases, berries successfully set but are not retained and tend to abscise before full maturation.

Most cultivated diploid potatoes and wild species are free-flowering types. However, many varieties in the cultivated tetraploids, among which conventional breeding activities are largely confined, produce only a few flowers. In several important varieties such as Bintje and King Edward, flowers are not normally found (Howard, 1970). This can be a serious drawback in breeding and/or genetical studies in that certain desirable crosses may not be possible to make

Two useful methods have been developed to prevent flower bud abscision and enhance its development. Carson and Howard (1954) successfully produced flowers in many varieties, including King Edward, by grafting potato scions on tomato stocks. Thijn (1954) developed the "brick growing" method to induce flowering. Briefly, the method involves growing the sprouted tuber on a brick or tile above soil level and covering it with sand. After the roots have grown into the soil, the sand is washed away thereby exposing the tuber-forming stolons which can then be cut before tubers fully develop.

Both aforementioned methods were designed to eliminate the sink (tubers) for carbohydrates and other assimilates produced by the haulm so that more nourishment is available for flower bud development. Howard (1970) further suggested the removal of axillary buds below the inflorescences for cv. King Edward and some other varieties because their development into shoots tend to compete with the inflorescences for nutrients. With certain potato varieties grafted on to tomato, aerial tubers sometimes profusely develop on or around the region of graft union (personal observation). When such sinks are produced, they should be promptly removed.



Fig. 9. A potato plant growing on brick to induce flowering. Note the exposed roots and mother tuber. Stolons at the base of the stems have already been cut to prevent tuberization.

Other treatments found conducive to flowering in potato are : long days (Patterson, 1953; Steineck, 1957), late planting (Rothacker, 1957) and gibberellic acid application.

Combination of treatments such as growing on bricks, long days and GA application may be necessary for certain clones that produce very sparse flowers (Anon, 1976a). The influence of moderately cool temperatures in enhancement of flowering should not be neglected either. The optimum mean temperature range for flowering in potato is about 16° - 18°C.

The full development of flowers among potato breeding stocks is no guarantee that all planned crosses can be achieved because many Tuberosum varieties are pollen-sterile. Fortunately, most pollen-sterile cultivars have good ovule fertility—ovule sterility appears to be rare. Pollen-sterile varieties can still be used therefore as females in the crossing block. Pollen sterility in potato is under genetic control and has been suggested to be due to a single dominant gene, or to recessive genes, or to gene-cytoplasm interactions (Okuno, 1952: Lamm, 1953; Ross, Peloquin and Hougas, 1964), the causes not mutually exclusive (Grun, Aubertin and Radlow, 1962; Grun and Aubertin, 1965).

Even if known ovule-fertile variety is pollinated by fertile pollen, there is still a tendency among some clones for flowers to abscise and thus, not produce berries. Peloquin and Hougas (1959) found that cutting the stems with flowers from field-grown plants and placing them in jars of water, sometimes containing an antibiotic for bacterial control, can be very successful. Use of nutrient solution does not appear to be necessary. The method allows controlled pollination to be done in the greenhouse where fertilization and subsequent development of berries are less prone to vicissitudes of environment. Wiersema (1950) recommended spraying the inflorescence with 2,4-D or other auxin analogues 2 - 3 days after pollination to minimize flower abscission and enable the ovaries to develop into seeded berries.

5.1.4.5 Other useful considerations

When clones are to be used frequently in crosses or in successive stages such as in a backcross program, it may be worthwhile to collect sufficient quantity of their pollen and preserve their viability for as long as possible. This technique will obviate the need of having parent clones flowering synchronously. Drying the anthers and then storing them at -20°C can preserve pollen viability for as long as two years (King, 1955; Howard, 1958). If subzero storage facilities are not available, storing pollen even at +2.5°C is sufficient to keep pollen alive for about a month (Blomquist and Lauer, 1962).

Storage of true potato seeds poses no difficult problem to breeders. Most potato seed samples, stored dry under normal laboratory conditions, can retain their viability for at least 10 years (Howard, 1978). Cold temperature (-20°C) storage can result in seeds remaining viable for at least 20 years (Howard, 1969; 1975).

As with tubers, true potato seeds exhibit dormancy. However, this resting period disappears after a few weeks in storage (Simmonds, 1963). Soaking dormant seeds in 2,500 ppm gibberellic acid for 48 hours, followed by drying, is effective in breaking true seed dormancy. However, germination is usually not nearly as uniform as seeds in which dormancy was naturally broken in prolonged storage. Howard (1978) observed that Tuberosum seeds stored for 9 months still retain a certain amount of dormancy and seeds stored for 21 or so months often germinate much better than seeds stored for only 9 months.

5.1.4.6 Systems of handling and selection of hybrid progenies

The ultimate goal of potato breeders is to identify and select the clones with the best promise of becoming exceptional cultivars. The variability upon which such selection is

applied becomes available either shortly after hybridization between parental clones, as in the case of pedigree breeding, or developed sequentially as in backcross and recurrent selection methods. As already noted, the penultimate derivatives from the latter breeding schemes are also handled via the same system as the pedigree method.

One of the fundamental prerequisities of successful plant breeding, regardless of which method is used, is the ability to recognize superior types from a limited or vast array of variability. It is here where the skill and keeness of the breeder's perceptive ability are put to a rigid test and where possibly, plant breeding as an art versus science is more than ever discretely manifested. Perhaps, it can also be said that it is here where plant breeding either makes or breaks. Afer all, potential variability left untouched is practically useless.

This section aims to present the activities in potato breeding from the time hybrid seeds are sown until a new variety is released.

5.1.4.6.1 Management of seedling and various clonal generations

Every potato seedling arising from botanical seed is practically virus-free because viruses, excepting spindle tuber viroid (Diener, 1971) are non-transmissible through seeds. As emphasized in Section 3, it is the breeder's task to preserve the selected clones in a virus-free state throughout the various stages of selection and multiplication. In order to insure that they remain so, certain techniques and precautions are considered standard measures in potato breeding.

Growing the seedling generation in an aphid-proof glasshouse or screenhouse is now a common practise where an effectively isolated, clean field to grow them cannot be found. Fig. 10 shows hybrid seedlings in 10cm diameter pots growing alongside virus-indexed clones inside a screenhouse. Combined with regular pest control measures to kill viruliferous aphids, effective soil sterilization, minimal handling of seedlings and proper sanitation including disinfection of hands, tools and other screenhouse equipment, seedlings can often be kept virus-free.

With freshly harvested seeds, dormancy should be broken by gibberellic acid treatment (see Section 5.1.4.5). However, germination is often not as uniform as those seeds whose dormancy had ceased after prolonged storage. The seeds may be sown on pans or other suitable containers, e.g. wooden flats, clay pots, etc., containing appropriate germinating medium. The medium could be sterilized ordinary greenhouse soil mix or if readily available, special sterile medium sold commercially, such as jiffy-mix. These special media, however, often need supplementary nourishment using Hoagland's or other nutrient solutions. When seedlings are large enough, they can be pricked into small plastic or clay pots where they are grown to full maturity.

When only a small amount of seeds are available and a maximum recovery of as many seedlings as possible is desired, seeds may be sown in Petri plates with moist blotting paper. As soon as seedlings have grown to a suitable size, they may also be pricked directly into pots. The size of pots may vary but 10 cm diameter pots are widely used. Pots that are too large permit production of larger tuber sets but effectively reduce the number of seedlings that can be grown per unit area. Smaller pots, on the other hand, will maximize the number of seedlings but tuber sets will be small.



Fig. 10. Hybrid seedlings (left) growing inside an aphid-proof screenhouse to keep them from being infected with viruses. A plastic strip below the pots prevent direct root-soil contact.

Care should be taken that non-random pricking of larger, rapidly germinating seedling is avoided. True seed dormancy and tuber dormancy appear to be correlated and could possibly even share a common biochemical pathway (Simmonds, 1964) and pricking out the rapidly germinating seedlings (short dormancy types) at the expense of late seedlings (long dormancy types) may result in unconscious selection for short tuber dormancy. Such problem could be acute especially when freshly harvested true seeds are sown without prolonged storage. In areas where short dormancy is desirable, the practise may be carried out or even further developed as a selection criterion.

The first clonal generation until the one prior to conducting small scale yield trials should be grown for further selection and multiplication in good seed districts to minimize the chance of viral infection. These areas are usually chosen for being spatially isolated from commercial production zones and/or where aphid populations are significantly low to enable the production of clean, healthy tuber seeds. Rigid pest control measures should also be practised to enhance the success of keeping the clones reasonably healthy.

The preliminary and subsequent yield trials naturally are conducted in commercial production districts and are aimed to compare the performance of selected clones against the leading cultivars. At these testing stages, the chance that clones will become infected is high and plans are usually made to insure an adequate supply of clean seeds for the various trials. A good scheme to multiply promising clones, once they are entered in variety trials or even a year or so earlier, should be an essential corollary activity that is closely tied up with the breeding program. Without such system, there is always the danger that promising clones may be selected against in the variety testing program due to virus infection. Breeders could greatly assist in the scheme by carrying out apparently healthy single plant selections from

promising clones and planting them out in individual rows to check their health. Infected progeny rows are then immediately destroyed and clean seed stocks are established only from healthy rows. These clean stocks can serve as buffer supply for further multiplication in case the clones unfortunately become infected during the various testing stages.

5.1.4.6.2 Methods of selecting superior clones

Potato breeders often must still deal with a number of important traits even though refinement of objectives had already been established. The necessity to have this multiplicity of selection targets is in large part enforced by the wide and sophisticated variety of usage that potato has come to nowadays. Even if a breeder delimits his goal to a specific type, the multitude of important disease and pest problems confronting potato producers hardly minimize the formidability of potential breeding objectives.

The objective traits naturally will vary in genetic complexity, some highly heritable and relatively easy to breed for, while others are complex and difficult. It is therefore only logical that proper selection pressures be applied at the appropriate stages of variety development. For example, it is ineffective to select for high yields or other complex traits at the seedling stage and in the first few clonal generations. Engel (1957) pointed out the large errors obtained when yields are estimated from observations on single plants or small clonal plots. Moreover, differences in the size of tuber set such as commonly manifested in the first clonal generation confound any possible selection even for relatively less complex traits.

Discarding seedlings that are too weak or too "wild" (types with long stolons and requiring short days for tuberization) may be 100% efficient according to Howard (1978). Contrary to Engel's (1957) findings, Verma (1972) concluded that it is safe to discard low yielding seedlings at the seedling stage itself. These low yielding seedlings are likely those which are weak, however. Maris (1962) and Howard (1963) both agreed that selection at the seedling stage should not be too stringent.

In the first clonal year, selection for such characters as tuber shape and depth of eyes may be efficient enough (Howard,1978). Heavy selection pressure in the first clonal generation, sometimes as high as 90% of the population, was questioned by Tai (1974) since plants in this generation are usually managed in an unconventional scheme (e.g. wide spacing vs. commercial practise). Using quantitative genetic analysis of data from two clonal generations (1st and 2nd), it was concluded that selection for quantitative traits in most cases is less efficient in the first clonal generation than direct selection in the second clonal generation. This corroborates more or less the conclusion of Engel (1957).

The Cornell program of selection among clones (Plaisted, 1966) will perhaps provide a sufficient example of how potato breeders manage the breeding materials when multiple objectives need to be attained. The program is multi-stage with three overlapping phases. In phase one, selection is emphasized for highly repeatable traits such as external appearance (e.g. tuber conformation, flesh/skin color, etc.) and resistance to golden nematode, a major problem in New York. Selection against highly undesirable traits such as after-cooking darkening is also practised even though they recur infrequently. In the second phase, selection for yielding ability of clones is undertaken, mostly based on the comparison of selections against one another but later on, towards the end of the phase, also against a standard check, cv. Katahdin, the principal variety in New York that is less prone to interactions with locations and season than other varieties. Finally, surviving selections are evaluated in the area where they are best adapted to and for the specific purpose for which they were developed. Table 6 provides further details of the Cornell program of selection

among clones generated from hybrid seedlings grown in 3 - inch pots in an aphid-proof glasshouse.

As may be noted, a range of only 0 - 2 clones is projected to remain and possibly be released as new varieties out of the original 30,000 seedlings (Table 6). Indeed, the probability of breeding a useful variety of potato is rather small (see Section 5.1.4.1.1). Hence, large number of seedlings must be raised and a quick, efficient selection scheme to choose the few superior types should be instituted. Raising large numbers of seedlings and producing large numbers of seeds from hybridization are easy enough to do. It is in the selection of seedlings and in the first few clonal generation when they are grown in small clonal plots that the most difficult practical problems in potato breeding are encountered (Howard, 1972).

An essential feature of the system that comes to light is the progressive emphasis and development in selection for yielding ability. From a cursory evaluation at a single location during the third year, the trial is expanded appreciably until in the 7th year and on, it covers six or more locations. It is very important that potato breeders conduct the trial over a number of seasons and locations because there are many economical traits, e.g. yield (Plaisted, 1960; Plaisted and Peterson,1959) , specific gravity (Haddock and Blood, 1939; Plaisted, 1957; and Stevenson *et al,* 1963; Thran, 1958), after-cooking darkening (Dalianis *et al,* 1966), flake quality (Isleib, 1962) and many others, which exhibit variety x season, variety x location, and variety x season x location interactions. Such interactions indicate that there is no predictable trend in the performance of clones over seasons and locations. Some varieties may do well at some locations and/or during certain season but not in others.

Without a certain amount of predictability, the choice of varieties, be they from hybridization or introduction, for recommendation becomes a complicated task. Breeders may surmount the limitations to selection imposed by genotype-environment interaction by restricting recommendations to a particular geographical location. Oftentimes, however, the bases for such recommendations are generally inconsistent. Moreover, it is not all that easy to clearly demarcate geographical areas. The breeder's alternative is to search for a variety which performs consistently over a range of locations and seasons (Akeley, 1958; Plaisted and Peterson, 1959; Plaisted, 1960; Harris, 1974; Tai, 1979). Stability of performance is a valuable attribute and, whenever possible, should be sought after. A cultivar which is widely distributed on account of its consistent performance certainly has demerits in regard to the dynamics of disease or pest epidemic but it greatly simplifies the variety situation, seed production and distribution problems, pest and disease management techniques, agronomic practices, and other important facets of commercial production.

In variety testing, it may be added that techniques could vary to a certain extent between country programs or even between regions within a country, viz. plot dimension, spacing, fertilization rate, cultural and management method, etc. Most, if not all, of these differences are partly dictated by the resource capabilities, needs, or even physical attributes of a particular geographical location. While these differences are inevitable, the multilocational tests within any program should follow uniform practices so that the trial results are comparable across locations and seasons. One might argue that differences artificially imposed during such trials would allow viewing the response of cultivars over a wider range of environmental diversity. On the other hand, the environmental factors even within a restricted locality are no doubt already broad and complex that any controllable variation taken out of any experiment helps in minimizing the complexity of results and facilitating their interpretations.

Other selection methods have been described by different workers (Black, 1953; Howard, 1978). Akeley (1966) described a practical breeding procedure for the development of potato varieties and seedlings with multiple resistance to a range of tuber disorders. While the described methods may vary to a certain degree, the underlying principles of selection in all cases remain the same.

5.1.4.7. Breeding for specific traits

As alluded to in Section 5.1.4.1., potato breeders in developing countries may concern themselves at the present time mostly with breeding for high yield and adaptation, resistance to pests and diseases, and to a limited extent, a few important quality attributes.

A slightly more detailed treatment of these breeding problems is given here, especially those relating to yield and adaptation, and resistance to two major diseases namely; late blight and bacterial wilt. Most programs in developing countries of the tropics have focused their attention to these problems (Anon, 1972). Available information did not indicate any major quality attribute under consideration elsewhere in these countries except the usual selection for the desired ideotypes of external appearance. These traits are, however, easily dealt with in breeding programs and need no extensive treatments here.

The distinct categorization of the breeding problems in this section should not give the notion that autonomous programs for each are realistic. In some cases, special emphasis perhaps may be given to some problems especially those which have proved difficult to solve, but eventually, all major objectives are integrated in the process of developing improved varieties.

5.1.4.7.1 Breeding for late blight resistance

No other disease of potato has probably wreaked more destruction on the crop, incited more fear in growers, and consequently, received more attention from scientists, than late blight. The blight epidemic of the 1840's in Europe which led to the infamous Irish famine provides glowing historical evidence to the notoriety of this disease.

The causal fungus, *Phytophthora infestans* (Mont.) de Bary, is so aggressive that if favorable conditions for its growth and sporulation continue, the disease progresses from the leaves to the haulm until this is completely destroyed, oftentimes in less than a month (Large, 1952). In temperate countries, the fungus overwinters in infected tubers until the next cropping season. In contrast, overlapping potato croppings throughout the year and presence of alternate solanaceous hosts provide a form of survival in tropical areas.

Late blight can be controlled by chemical means or through the use of resistant varieties. Preventive fungicidal sprays working hand in hand with efficient blight forecasting, sanitary practices such as destruction of discarded infected tubers and volunteers, and legislation regulating the use of blight-free tuber stocks for planting, have been very effective in minimizing yield losses in developed countries even with the use of highly susceptible cultivars. In developing countries of the tropics where potatoes are farmed mostly on small landholdings, farmers oftentimes cannot afford to spray regularly for lack of capital and/or inavailability of materials and equipment. Moreover, potatoes in the tropical countries are mostly grown in the highlands during the rainy season-a factor which introduces a difficult dimension in controlling the disease by the use of fungicides. The use of resistant varieties thus offer the brightest promise for the control of late blight in these regions.

Table 6. Details of the Cornell program of selection among clones (modified after Fig. 4 of Plaisted, 1966)

Year	No. of clones	No. of site	Locale	No. of reps	Plot length (ft)	Between-hill spacing (inch)	No. of plants/ plot	No. of select-ions	Traits under selection
1	30,000	1	isolated field	1	3	40	single hill	1,500	Highly repeatable traits, e.g., external appearance, golden nematode resistance and after-cooking darkening
2	1,500	1	"	1	10	10	12	200	Appearance, tuber size and set, specific gravity, after-cooking darkening and chipping ability
3	200	1	commer-cial area	4	15	10	18	70	Appearance, specific gravity, after-cooking darkening, chipping ability, scab and Verticillium wilt resistance and for the first time, yielding ability
4	70	2	"	4	15	10	18	25	Same selection forces as above but selection for yield becomes predominant
5	25	3	"	5	20	10	24	10	Further selection for yield
6	10	4	"	5	2x20	10	48	3-5	Same as above but in larger plots and more locations
7	3-5	6	"	4	2x20	10	48	3-5	Same as the above but in more locations; to accommodate increase in locations, reps within locations are reduced
8	3-5	6	"	4	2x20	10	48	0-2	Repeat of year 7 trial for better sampling of locations and seasons
9	0-2	6+	"	4	2x20	10	48	0-2	Repeat planting of surviving selections in 6 regional locations, in addition, separate evaluation trials where selections are most appropriate are conducted
10	0-2	6+	"	4	2x20	10	48	0-2	Same as above

11	0-2	6+	"	4	2x20	10	48	0-2	Same as above;after the year 11 trial, preparations for subsequent release of best clones are made

Two different genetic systems control late blight resistance. The first type, conditioned by a series of major genes (so-called R-genes) imparts a hypersensitive reaction in the host causing the cells surrounding the initial point of pathogen invasion to die. This reaction effectively localizes the pathogen to the area of its initial entry and subsequently is unable to survive. The major R-genes come from the wild hexaploid species, *S. demissum*, widely distributed in Mexico. There are so far 11 known R-genes, designated R_1 to R_{11}.

Black (1952) and Black et al (1953) worked out the genetical basis for classifying races of *Phytophthora infestans* based on the specific gene-for-gene relationship between the major resistance genes in the host and the virulent factors in the parasite. Accordingly for example, a variety such as Kennebec which carries the gene R_1 is resistant to races 0,2,3,4, but susceptible to races 1, 1.2, 1.3 and on (as long as the complex race carries the virulence factor able to overcome the resistance of gene R_1). Resistance, in other words, is specific to a particular race.

The major R-genes have been very useful in providing clean potato crops until new races able to overcome them evolve. Experience shows that this form of resistance is quite unstable. Clones with two or more R-genes have been bred but a new race always comes along in a few years to make the clones practically useless. The extreme variability of *P. infestans* no doubt makes the use of race-specific form of resistance only of temporary value. For this reason, breeders have now shifted to the use of another form of resistance called "field resistance" (or horizontal, non-race specific, general resistance).

Black (1970; 1972) defined field resistance as the "degree of resistance exhibited by a plant to all races of the parasite". It is inherited in polygenic fashion and various minor genes involved appear to supplement each other in the control of the disease. In individual plants, these minor genes determine : degree of resistance to infection, rate of disease spread after infection, the time required for the onset of sporulation, and the number of spores produced.

Based on the reaction of seedlings tested under controlled conditions, five resistance groups may be identified according to the amount of damage seven days after inoculation (Black, 1970). Using the system, Black (1970; 1972) was able to show that when both parents are group 1 types, the proportion of group 1 and group 2 seedlings are generally much higher, even reaching a combined proportion of 70% in some progenies (Table 7). Since these reaction types do not normally require protective spraying, the proportion of resistant seedlings available for selection of commercially important attributes is satisfactorily high.

Wild Mexican species such as *S. demissum, S. phureja, S. verrucosum, S. bulbocastanum, S. pinnatisectum, S. cardiophyllum* and *S. trifidum* have been indicated as the best sources of field resistance. *P infestans* originated in Mexico and adjacent areas, and the long, intimate association between the host species and the highly variable parasite there must have provided the best opportunity for natural selection to develop the gene pool necessary for stable resistance. Of the above species, *S. demissum* appears to have the best prospect because it crosses readily with *S. tuberosum* and, as indicated earlier, has been widely used by plant breeders throughout the world as source of R-genes. The resistance

among some of the other species may not be easily utilizable on the other hand because of their barriers to hybridization with *S. tuberosum*. Hermsen and Ramanna (1973) have provided however some hope in the hybridization work with *S. bulbocastanum*. A fairly low level of field resistance is also available in some species from South America, e.g., *S. tuberosum* ssp. *andigena, S. phureja, S. commersonii, S. acaule, S. spegazinii, S. curtilobum*, and others.

The multigenic control of field resistance and its complex expression counteract the flexibility in the aggressiveness of *P. infestans* (Umaerus, 1973). As a result, resistance is more long-lasting and stable than the race-specific resistance. Experience from the long term field testing in Toluca Valley, Mexico (an area where a complex of races is present and the only place known where sexual hybridization in the pathogen exists thus providing it with a very important mechanism for genetic change in response to the change in the host) has indicated no sudden changes of field resistance.

Table 7. Blight resistance in hybrid progenies (selected from Tables 2 and 3 of Black, 1972)

Reaction of parents[a]	No. of seedlings tested	Distribution (%) in reaction groups				
		1	2	3	4	5
1+x4-	202	4	16	33	29	18
1 x2+	210	10	6	22	38	24
3 x1	145	17	12	32	33	6
1 x3	167	12	24	25	35	4
1 x1+	125	22	46	14	10	8
1 x1+	131	17	56	15	10	2
1 x1	137	36	33	16	12	3
1 x1	180	28	41	23	6	2

[a] Group 1: restricted lesion, 3% area infected=highly resistant
2: partly restricted, 10% area infected=fairly resistant
3: retarded lesion, 30% area infected=slightly resistant
4: normally progressive lesion, 60% area infected = normally susceptible
5: rapidly progressive, 100% area infected = very susceptible
- : indicates that the reaction is on the resistant side of group while;
+: indicates that the reaction is on the susceptible side.

While stability of field resistance is an attribute that breeders ideally look for, the very fact of its complex manifestation and polygenic control make it a difficult trait to breed for. Large numbers of individuals need to be handled and hence, a practical, yet effective screening method is an essential requirement. Umaerus (1970) developed a screening test based on the finding that plants with low infection frequency also require a long inoculation access period (period of free water on the leaf surface and optimum temperature for spore germination and penetration). This character is apparently manifested in the seedling stage. Screening techniques emphasizing certain post-infectional factors, (e.g., fungal growth rate, rate of necrosis, generation time, and sporing capacity) have been used by other workers (Estrada and Guzman, 1969, Black, 1970; Young *et al*, 1972). In these methods, visual disease index measurements of disease progress serve as the selection criterion.

As may also be expected from the nature of genetic control, the expression of field resistance is highly influenced by non-genetic factors such as ontogenetic development of the plant, daylength, light intensity, and mineral nutrition. For example, blight tests for field resistance in Mexico, where photoperiod is short, using clones developed for the long days in temperate countries are often found to be too severe. Materials are ranked as more susceptible under short day conditions than they are under long day conditions. Nevertheless, breeding field resistant clones adapted to short days and higher temperature is not necessarily precluded as experienced in Kenya (Black, 1972). Late maturity and field resistance also appear to be correlated but does not preclude the combination of early maturity and resistance. The predisposing effects of increased potassium and decreased magnesium levels on certain resistance components such as lesion growth and sporulation intensity have also been reported by several workers (cf. Umaerus, 1973). High nitrogen nutrition is also associated with increased resistance under certain conditions. Broadly speaking, the influence of various environmental factors on field resistance clearly stresses the need to maintain as uniform conditions as possible during the screening period in order that genetic differences among clones are reasonably accentuated.

Breeding for field resistance can be easily complicated by the presence of major R-genes. To avoid this difficulty, breeders must either work on clones without a known major gene or test the breeding materials in locations where many races are present. The latter should enhance the chance that compatible races of the fungus matching the possible R-genes in the breeding materials exist. As already noted, such a place is the Toluca Valley in Mexico. Indeed, breeding for field resistance has been greatly facilitated using the facilities in that site (Niederhauser and Cobb, 1959; Cervantes, 1965; Lapwood, 1971).

Resistance to late blight in the foliage appears to be positively correlated with that in the tuber. Still, there are quite a large number of varieties with susceptible foliage but moderately resistant tubers. On the contrary, Howard (1978) noted that many cultivars with major R-genes for foliage resistance have very susceptible tubers.

Breeding for tuber resistance has been largely neglected although a substantial degree of varietal differences exists (Cox and Large, .1960). Part of this apathy comes from the difficulty of developing a reliable and practical screening method. Techniques of evaluating tuber resistance requiring few replicates have been devised-one method measures the frequency of infection after inoculation either by spraying whole tubers or pipetting the inoculum into the eyes while another measures the rate of mycelial growth through the internal tuber tissues. Langton (1972) claims good correlation with field resistance when tuber resistance is adjudged through a combination of the two methods. The criterion of resistance was the frequency of infected cores of tuber slices inoculated through wounded eyes combined with the average time it takes the fungus to appear on the uninoculated surface.

Umaerus (1973) emphasized the need to breed varieties with late blight resistance both in the foliage and the tuber. This is especially critical if the variety bred carries field resistance in the foliage-a situation where the pathogen is sustained for a longer period in the plant, thereby increasing the possibility of extensive damage to the tubers if tuber resistance is not present.

5.1.4.7.2 Breeding for bacterial wilt resistance

Bacterial wilt caused by *Pseudomonas solanacearum* (E.F. Smith) is common in many tropical and subtropical countries (Thurston, 1963). The disease can develop very rapidly

and be very destructive especially when temperature, rainfall, and relative humidity are favorable for its development. Crop losses of 100% are not uncommon and it is estimated that, were the disease to be controlled, potato cultivation would be increased ten-fold (Robinson, 1968). Bacterial wilt attacks not only potato but also other solanaceous and non-solanaceous crops such as tomato, tobacco, peanut and banana (Quiñon *et al*, 1964; Lozano and Sequeira, 1970; Granada and Sequeira, 1975).

Three distinct pathogenic races are recognized-race 1 attacks tobacco, tomato, eggplant, potato and other solanaceous crops; race 2 causes wilt in banana and *Heliconia* sp. but does not attack potato; and race 3 is pathogenic to potato and tomato but weakly pathogenic to other solanaceous species. Thus, only race 1 and 3 attack potato in nature. Race 3 is common in the highland tropics and can cause disease at a lower temperature threshold than other strains (Thurston, 1963). On the other hand, race 1 is widespread in both tropical and subtropical lowland areas (Sequeira and Rowe, 1969).

Effective and economical means of controlling bacterial wilt, apart from long-term cultural practices as crop rotation and field sanitation, have not been developed so far. Resistant varieties still offer the most economical way to minimize its destructiveness. Useful levels of resistance have not been found until Thurston and Lozano (1968) discovered that certain clones of Colombian *S. phureja* showed high levels. Resistance, however, is apparently uncommon—only 6 resistant clones were identified out of 1,061 tested. Sequeira and Rowe (1969) confirmed the resistance of the above clones against 10 isolates of *P. solanacearum* in greenhouse and growth chamber studies. The reaction of clones ranged from resistance to only one isolate (K-60) up to resistance to all isolates.

Recent breeding efforts have concentrated mainly on the transfer of *S. phureja* resistance to *S. tuberosum* although occasional resistance has also been reported in other species (Robinson, 1968; Thung, 1947). It appears that resistance can easily be incorporated to *S. tuberosum* (Gonzales *et al,* 1973; Rowe and Sequeira, 1972). However, resistance of clones varied not only with the virulence of the isolates of *P. solanacearum* (Gonzales *et al,* 1973) but also with temperature, varieties being more susceptible at higher temperatures (French, 1972; 1973). Table 8 clearly demonstrates the variation in cultivar reactions across different isolates and temperature regimes.

It can be seen that cultivars 1386.15 and 1386.26, both *S. phureja* cultivars from Colombia, were the most resistant across all isolates although they showed only tolerance at warm temperature regimes to the two most virulent isolates, S 213 and P1. It is worthy to note that these virulent isolates originated from tropical countries-S 213 was collected from Paraiso, Costa Rica and P1, from Chiquirip, Peru. On the other tand, less virulent isolates such as S 245 and K 51 came from temperate countries, Australia and United States, respectively.

The apparent ease with which the transfer of wilt resistance from *S. phureja* to *S. tuberosum* has been accomplished owes a great deal from the fairly simple genetic control of the character. Rowe and Sequeira (1970) concluded that resistance (to isolates K 60 and S 213) in *S. phureja*, based on reaction of diploid hybrid progenies from crosses between resistant and susceptible clones, is controlled by two dominant and independent genes for each isolate and by a common gene. This result is largely corroborated by genetic studies at the tetraploid level using as resistant parents, one 4x derivative clone from the cross *S. phureja* with *S. tuberosum* and an unrelated clone selected from the University of Guelph populations (Opeña *et al,* 1979; unpublished). Field tests of progenies derived from *S. phureja* (2x) x *S. tuberosum* (various dihaploid and tetraploid clones) also showed that high

Table 8. Reaction[a] of potato cultivars inoculated by soil infestation with isolates of *P. solanacearum* after incubation for 29 days at two temperature regimes (adapted from Table 1 of French, 1972)

		Cultivars					
Isolate	Temp. °C	1386.15	1386.26	V-7	6-5	59.B5-1	BR-6014
P1	28/16	T	T	S	T	S	S
	20/ 8	T	R	T	R	R	S
S 207	28/16	R	T	R	T	S	T
	20/ 8	R	R	R	R	R	R
S 213	28/16	T	T	S	S	S	S
	20/ 8	R	R	T	T	T	S
K 51	28/16	R	T	R	T	R	R
	20/ 8	R	R	R	R	R	R
S 245	28/16	R	R	R	T	R	R
	20/ 8	R	R	R	R	R	R
K 197	28/16	R	T	R	T	R	T
	20/ 8	R	R	R	R	R	R
K 56	28/16	R	T	T	T	S	S
	20/ 8	R	R	R	R	S	T

[a] R = resistant; T = tolerant; S = susceptible

levels of resistance have been transferred from *S. phrueja* ; indirect proof that resistance is rather simply inherited (Anon, 1974).

Results of previous studies (Sequeira and Rowe, 1969; Rowe and Sequeira, 1970; Rowe *et al,* 1972) imply that resistance to bacterial wilt may be race-specific (analogous to the major R-genes for late blight resistance). If so, there exists the danger that resistance may not be stable vis-a-vis a variable pathogen. Using epidemiological techniques based on van der Plank's (1963) analysis of plant disease epidemics, Robinson (1968) found clones which appear to exhibit vertical (race-specific) resistance, horizontal (non-race specific) resistance, or both. Based on a number of considerations such as high rate of stabilizing selection in *P. solanacearum*, its simple interest rate of increase, and its possibly high vertical mutability, it was further concluded that vertical resistance may remain agriculturally valuable for one growing season only but, given the proper rotation and use of wilt-free seeds, it would, in a wider sense, endure indefinitely. While Robinson (1968) dismissed his results as preliminary, there seems little doubt that vertical resistance to *P. solanacearum* does occur in potatoes.

The question as to which type of resistance would be most useful to combat bacterial wilt obviously needs more thorough investigation. If its analogy to the late blight situation is complete, then the sad experience with late blight will show that horizontal resistance is the most rational goal. The accompanying difficulties of breeding horizontally resistant clones will have to be taken into account by breeders. Where management practices such as effective rotation and regulated use of clean seeds can be enforced, the relative ease of breeding for vertical resistance may be enough to offset its disadvantages.

5.1.4.7.3 Breeding for high yield and adaptability

There is a definite truism to the statement that one of the best ways to develop high yielding cultivars is to breed for disease and pest resistance. However, quite apart from abiotic factors, yield *per se* is a distinct character resulting from a number of interacting yield components and consequently, quite complex in expression, under polygenic control, and easily prone to environmental effects. Pests, diseases, and other abiotic factors only serve to influence the final expression of yield. Yield, as a breeding objective, is therefore one of the most difficult that breeders have to contend with.

Simmonds (1969) considered two basic requirement in designing a potato breeding program after realism in the choice of objectives has been exercised—first, breeders need a rational choice of parents and breeding patterns, and second, efficient selection methods should be available. When dealing with oligogenically controlled characters, the known methods are fairly straight-forward and they are relatively easy to deal with. But many economical characters, including yield, are polygenic and of which, the biometrical genetic bases are rather limited, apart from being too complicated. By necessity, much of the choice of parents therefore proceed largely by instinct-"crossing the best with the best and hoping for the best".

Potato breeders work in either of two directions. They may cross an elite clone with a wide range of other clones and assume that the common parent has a fairly high level of general combining ability. In another case, specific combining ability is assumed and breeders usually explore a large number of crosses and then keep only the promising few for further exploitation. Progeny testing methods to detect variation among clones in combining ability are of course now available. Further biometrical genetic investigations of the economical characters in potato should serve to provide breeders with more guidance in the choice of best breeding approaches.

Selection techniques for yield or other complex characters in potato have been discussed earlier (Section 5.1.4.6.2). The sequential method of selection generally practised by potato breeders i.e., taking the highly heritable characters first during the early stages of selection and the complex ones later, is not only realistic but also logical. Engel (1957) pointed out the fallacy of selecting for yield and other complex characters in the seedling generation and in small clonal families. An ideal selection method when several traits are simultaneously considered is through the use of a selection index which often takes into account an economic weight for each trait under selection. However, this approach is dismissed by many potato breeders as too impractical and laborious to be a realistic procedure.

Potato generally behaves as an outbreeder although self-fertilization is possible. Successful clones, almost automatically those with high yield and good adaptability, are highly heterozygous and presumably heterotic. Breeding methods to improve yield and adaptation is therefore geared towards attaining maximum heterosis in breeding populations in order that chances of recovering outstanding clones are improved. Experience with other crops such as maize and the theory of gene action indicate the importance of genetic diversity for greater manifestation of heterosis.

By and large, the total potato breeding effort in temperate countries has increased enormously since 1910, the acknowledged end of the heyday of potato breeding. Although some notable variety releases have been made since, e.g. Katahdin in USA, Ackersegen in Germany, Voran in Holland, Arran Pilot in England, and a few others, Simmonds (1969) considered the accomplishments of modern breeding incommensurate to the overall scientific

inputs to potato improvement. The narrowness of genetic diversity in Tuberosum breeding stocks has been pinpointed as the major limitation. More recent potato breeding efforts have emphasized the infusion of genetic diversity into the current Tuberosum gene pool and the use of the Andigena group for this purpose has received the greatest attention.

The Andigena potatoes are short-day adapted types. When grown during the long, summer days of temperate countries, they tend to be late-maturing and unproductive. Moreover, they generally show poor tuber shape, deep eyes, poor resistance to diseases, excessive vine growth, narrow leaves, poor canopy, etc. Nonetheless, it is now widely recognized that the present day Tuberosum gene pool evolved from a limited introduction of Andigena clones into Europe during the early part of the 16th century (Salaman, 1946; Salaman and Hawkes, 1949; Salaman, 1954) and is a magnificent tribute to its enormous store of genetic potentiality for improvement.

Because of the undesirable features of Andigena potatoes, Andigena (A) x Tuberosum (T) hybrids almost invariably result in a low frequency of selection but a higher potential for yield. In order to enhance the commercial potential of AT hybrids, preliminary selection in Andigena is needed to remove the undesirable portion of variability (Glendinning 1969). AT hybrids using unselected Andigena are generally too late to reach their yield potential. Thus, although heterosis is theoretically maximum in the immediate F_1, some sacrifice in terms of accompanying loss of heterosis (brought about by progressive narrowing of variability due to selection) is a necessary compromise in order that variation in AT hybrids will overlap with commercial requirements. Just how much this sacrifice will be remains to be seen. Using selected Andigena clones in crosses with Tuberosum, the mean progeny advantages of AT hybrids over intra-Tuberosum hybrids tested in temperate regions were still impressive (Glendinning, 1969; Cubillos and Plaisted, 1976; Tarn and Tai, 1977). Thus, the predicted heterosis in yield expected from infusion of variability from Andigena to the Tuberosum gene pool is unquestionably there to exploit.

The basic objection to the utilization of Andigena in previous breeding efforts in temperate regions, apart from its lack of adaptation to long days, is its extreme susceptibility to diseases, notably late blight. The mass selection programs in Andigena populations at Pentlandfield, Scotland (Simmonds, 1969) and at Cornell University (Plaisted, 1972) have not only yielded advanced clones with yielding capacity and maturity that are comparable with Tuberosum clones but, on the average, they are somewhat better in terms of late blight resistance. For example, the 5th cycle of the Cornell population tested in Toluca, Mexico in 1973 showed 37% with high levels of field resistance. The variability of Andigena populations has also yielded clones with resistance to PVY, PVX, common scab, *Verticillium* wilt, aphids, leafhoppers, golden nematode, root knot nematode, etc. The progress that had been achieved in the Andigena selection program and their exciting breeding possibilities offer the present-day potato breeders a broad new horizon to improve potatoes beyond the levels attained by their 19th century predecessors.

The continuing use of mainly Tuberosum cultivars for potato improvement in developing countries has been suggested earlier as a potentially unrewarding approach (Section 5.1.1). While it is true that most successful cultivars in many of these regions are Tuberosum types (especially late maturing maincrop varieties of the temperate zones), the prospect of further replacing them with more highly selected Tuberosum clones from local or foreign breeding programs is not good in view of the limited genetic diversity of the Tuberosum gene pool. In its stead, the utilization of Andigena gene pool and the hybrids of preselected Andigena clones, or Neotuberosum in Simmonds' (1969) terminology, with

locally adapted Tuberosum cultivars may very well be a more productive approach. Simmonds (1971) even ventured to suggest that major efforts to adapt the potato to a climate different from its own habitat, e.g., hot, humid tropics, should look at the useful genetic variability in Andigena rather than attempt to find adapted types from highly selected Tuberosum clones. If the new regions are marginally suited to Tuberosum, the use of hybrids between Tuberosum and selected Andigena clones may provide the greatest opportunity for success (Plaisted, 1972).

5.2. Non-traditional breeding methods

Although almost all *S. tuberosum* cultivars grown today have been developed through conventional breeding (introduction, hybridization and selection), an exceptional few arose as bud sports (somatic mutation) from established varieties and have since been adopted by farmers whenever they were found economically important. For example, Howard (1970) estimated that in 1968 in England, there were 20,000 acres grown to Red Craigs Royal compared to about 6,000 acres of its original type, Craigs Royal. Other examples of bud sports that have become established cultivars are Red Pontiac, derived from variety Pontiac, and Red La Soda, which originated from variety La Soda (Anon, 1967).

In addition to mutation breeding, new methods and other exciting areas of development are being explored by potato scientists around the world. The potential use of dihaploids in breeding has occupied much research attention since the pioneering work at Wisconsin of Hougas and Peloquin (1958) on generating them in higher than normal frequencies. The use of botanical seeds in actual commercial production instead of tubers has recently received some research impetus. This has an obvious potential for developing countries without a good seed program. Apart from these, more sophisticated approaches such as protoplast fusion are opening new vistas for further potato development.

It is the purpose of this section to present relatively briefly these non-traditional methods in order to broaden the perspectives of researchers engaged in the field of potato improvement and update their knowledge of the scientific developments therein.

5.2.1 Potential use of dihaploids in potato breeding

Dihaploids are diploid plants derived through parthenogenesis from tetraploids. Potato dihaploids (2n=24) have been known since the 1930's but they occurred rather infrequently. It was not until the discovery of Hougas and Peloquin (1958) that certain diploid *S. phureja* pollinators on female tetraploid Tuberosum and Andigena clones can increase their frequency that interest on the potential use of dihaploids in breeding was greatly intensified.

Later studies (Peloquin et al, 1966) showed that the dihaploid frequency can be further increased by using the cut stem method for flower production and subsequent pollination in the glasshouse (see also Section 5.1.4.4), and by choosing superior pollinators from *S. phureja*, particularly Pollinators 1.1, 1.3 and 1.22 selected from *S. phureja* clone PI 225682. Hermsen and Verdenius (1973) improved the method further by using a genetic marker, embryo spot, which facilitated the identification of dihaploids from 4x-2x crosses.

Hougas *et al* (1964) observed that selected pollinators can give dihaploid frequencies of about 10 per 100 berries in crosses with a wide range of female parents in contrast to an average for other pollinators of only one dihaploid per 100 berries. Hanneman *et al* (1978) observed more or less comparable frequencies (13 dihaploids per 100 berries) from Group Andigena. The superior pollinator effect appears to be simply inherited with either one or a few recessive genes involved (Peloquin *et al,* 1964).

The influence of female parents on frequency of dihaploid production is also significant, clones such as Merrimack and Wis. Ag. 231 averaging 10 dihaploids per 100 fruits compared to just over one for other seed parents (Hougas *et al,* 1964). Frandsen (1967) observed an interaction however between seed parents and pollinators.

When tetraploid seed parents (4x=48) are pollinated by *S. phureja* diploid pollinators (2n=24), it is expected that triploid progenies (3n=36) will be produced, However, results showed that these triploids are produced in surprisingly low numbers, the majority being tetraploids (arising from fertilization of 2n egg cell of tetraploid seed parent by unreduced 2n pollen of the pollinator) and the minority are diploids. There appears to be a triploid block in 4x-2x crosses (Marks, 1960). The diploids (or dihaploids, in the sense that they are haploids of tetraploids) have been genetically shown to be maternal in origin, derived from unfertilized egg cells which developed parthenogenetically. Further studies (Wangenheim *et al,* 1960; Bender, 1963) showed that dihaploid embryos (24 chromosomes) were regularly associated with hexaploid endosperm (72 chromosomes) instead of the expected pentaploid endosperm (60 chromosomes). Based on indirect evidence, it has been suggested that a superior pollinator is one which contributes two 12-chromosome male gametes leading to the development of hexaploid endosperm (48+12+12=72 chromosomes). In the process, no male gamete is available to fertilize the egg cell (24 chromosomes). Parthenogenetic development of these unfertilized egg cells thus gives rise to dihaploid plants.

Dihaploids are generally weak (Wohrmann, 1966) as may be expected from the genetical consequence of their derivation—generating dihaploids from tetraploids is equivalent to three generations of inbreeding the tetraploids. Krantz (1946) showed that tetraploid potatoes behave genetically as an outbreeder and exhibit inbreeding depression upon selfing, although at a rate slower than inbreeding of diploid species. Occasionally, some dihaploids appear to be as productive and vigorous as their parents. Hybrids between Tuberosum dihaploids and diploid species *S. phureja* also showed improved vigor and yield (Hougas and Peloquin, 1965; Rowe, 1967a).

Most dihaploids are pollen sterile but a great majority have been found to be slightly female-fertile. Caroll and Low (1975) observed considerable reduction in female fertility of first generation dihaploids of *S. tuberosum.* In some cases, dihaploids also produced flowers with some difficulty. For example, of the first 60 dihaploids produced, 53 flowered of which 30 were female fertile but only 5 had viable pollen (Ross *et al,* 1964). Pollen infertility obviously may be a serious barrier to the utilization of dihaploids. However, crosses between dihaploids with other diploid species or among themselves can increase not only pollen fertility but also vigor and productivity of the resulting progenies (Ross *et al,* 1964; Hougas and Peloquin, 1965; Rowe, 1967a; Tiemann, 1976). There are also indications that dihaploids from Group Andigena have better male and female fertility than those from Tuberosum (Landeo and Hanneman, 1979).

Several methods have been proposed to use dihaploids in potato breeding. Hougas and Peloquin (1958) presented most of the arguments in favor of doing the genetic and breeding studies at the diploid level as contrasted to the tetraploid level. Chase (1963) suggested a ten-step analytical breeding scheme where intensive inbreeding and selection are done at the diploid level followed by resynthesis of the tetraploid forms. The evidence on the question of the need to return to tetraploid level for commercial production is conflicting.

Rowe (1967) compared 11 diploid with 11 tetraploid hybrid families and concluded that gene action and heterozygosity may have a greater influence on vigor and productivity than ploidy level. The tetraploid hybrid families (from *S. phureja* x Tuberosum dihaploids)

yielded better than diploid families when established from botanical seeds. However, this advantage disappeared when both were propagated from tubers. Diploid families also showed greater variability which indicated that they could respond to selection faster than tetraploids. In another paper, Rowe (1967b) found that diploid clones from *S. phureja* x Tuberosum dihaploids generally performed better than their vegetatively doubled counterparts.

On the other hand, Mendiburu and Peloquin (1971) produced tetraploids via sexual polyploidization (4x-2x and 2x-2x crosses in which unreduced gametes functioned) instead of vegetatively doubling the chromosome number and found that these clones outyielded their diploid "full sibs" by 50 percent. Chase (1963) suggested the resynthesis of tetraploids via unreduced gametes as an alternative to vegetative doubling. Sexual polyploidization does not involve inbreeding while vegetative doubling is approximately equivalent to two generations of selfing a tetraploid (Haynes, 1972). Thus, Rowe's (1967a) data indicating the inferior performance of the vegetatively doubled counterparts of diploid clones may have been largely due to inbreeding depression.

Regardless of the above controversy, the relative genetic simplicity of dihaploids compared to tetraploids and its consequence in genetical and breeding work is an overwhelming opportunity that potato scientists should attempt to exploit. However, if potato breeding is to be carried out at the diploid level, there is an urgent need to assemble the necessary diploid parents, particularly since the fertility of dihaploids is low and selection for fertility as well as for the desired characters have to be done (Howard, 1978). This problem appears to be surmountable as intercrosses among dihaploids or their crosses with cultivated *S. phureja* do show improved vigor and fertility (Ross *et al,* 1964; Hougas and Peloquin, 1965; Rowe, 1967a; Howard, 1970; Tiemann, 1967).

With regards to crosses of dihaploids with other diploid species, Simmonds (1966) argued that any population of Tuberosum dihaploids is genetically narrow-based like their source gene pool and so would have little potential for improvement ; therefore, a program of infusing genetic variability from diploid species into the population of Tuberosum dihaploids along the line of the Andigena program is clearly necessary. Already, mass selection programs among widely based South American diploid stocks are underway (Simmonds, 1969; Haynes, 1972) so that eventually, more commercially desirable hybrid progenies between these improved diploid stocks and the Tuberosum dihaploids may be possible to select. Haynes (1972) pointed out, however, that direct utilization of improved diploid cultivars, particularly those from cultivated species *S. phrueja* and *S. stenotomum*, should not be neglected. Most of the diploid clones grown commercially in South America are largely unimproved and its great potential for production has heretofore been unexploited. He cited not only the more rapid response to selection expected on diploids as a major advantage but also the opportunity of isolating more productive genotypes for specific environments.

Even assuming that breeding at the diploid level will turn out to be not as promising as everyone hopes, the synthesis of useful tetraploid breeding stocks via dihaploids should have immediate significance (Simmonds, 1969; Howard, 1970; Howard; 1978). For example, a dihaploid clone carrying a dominant gene for resistance (either in single or double dose) can be vegetatively doubled using colchicine to produce tetraploid stocks which carry that particular gene in duplex or quadruplex form, as the case may be. Using such stocks in breeding at the tetraploid level, rather than the simplex clones more commonly available to the breeder, provides considerable gain in efficiency. It can be shown easily that quadruplex and duplex stocks crossed with nulliplex clones will yield 100% and 83% hybrid progenies with

the desirable dominant gene, respectively. In contrast, simplex clones in similar crosses will give only 50% desirable progenies. This argument has been extended by Howard (1978) to relatively more complex quantitative characters. Clearly, the number of progenies to handle in the breeding program can be significantly reduced using such specially synthesized stocks. There are indications that improved levels of disease resistance can be found among dihaploid stocks (Alam and Peloquin, 1971; Cipar and Lawrence, 1972; De Maine, 1978). Therefore, synthesis of special tetraploid stocks is a possibility.

5.2.2 Mutation breeding

Mutation can be roughly described as heritable genetic changes either occuring naturally (spontaneous mutation) or artificially induced (induced mutation) by mutagenic agents such as radioactive rays or chemicals. As mutation contributes to genetic variations which serve as the raw materials for selection, their potential use in breeding has also been explored in some crop species. Stebbins (1950) considers mutation as the ultimate source of variation between two individuals.

In potato, a few cases of bud sports (somatic mutations) that have led to the development of commercially accepted cultivars have been cited earlier. Artificial induction of mutations as a tool in potato breeding has not been generally well accepted, however, even though the methods have greatly developed since the discovery as early as 1935 by Asseyeva and Bladigova that X-ray can provoke mutations in potato. Now, mutations in potato can be induced by a wide range of agents : physical agents apart from X-ray are P^{32}, gamma rays, and more recently, neutrons (Solomko, 1965; MacCrory and Grun, 1969; Van Harten, 1972; Gomez Cuervo and Estrada, 1972; and Miedema, 1973); chemical agents such as ethyl methanesulfonate (Ferwerda, 1965; Umaerus, 1966); ethyl imine, diethyl methanesulfonate, N-nitrosomethylurethane, etc. (Nayar and Chauhan, 1968; Jauhar, 1969; Pavek, 1972; Upadhya and Purohit, 1973).

The lack of interest in induced mutation as a breeding tool in potato may be attributed to prejudices, irrelevant arguments, and a considerable amount of conservatism among potato breeders and some scientists (Van Hartin, 1978). Nonetheless, he did admit that, 40 years after the discovery of mutation-inducing ability of X-rays in potato, not much has been achieved in practise. Notable exceptions are the release of cv. Konkei 45 with improved tuber skin color in 1973 in Japan and the reported release to Soviet farmers of some cultivars with improved resistance to late blight derived from gamma-irradiation (Anon, 1973).

Several reasons have been given to account for the lack of success of mutation breeding (Van Harten, 1978). Technical problems always appear foremost in the argument. If mutation breeding is to be a practical tool in potato improvement, many diverse mutations must be produced and if they can be obtained, the method may seem at least as promising as handling thousands of hybrid seedlings (in conventional breeding) of which really only a few or even none leads to a new cultivar. It has been proven by several workers (Heiken, 1960; Anon, 1963; Nayar, 1969; Nayar and Dayal, 1970) that high frequencies of induced mutations can be obtained. For example, Heiken (1960) obtained 37% mutated plants at a dose of 2,000 - 3,000 R of X-rays but even as high as 50% is achievable (Nayar and Dayal, 1970) by periodically removing and separately planting the sprouts from irradiated tuber halves. From these results, low frequency of induced mutations cannot be the limiting factor in the practical application of mutation technique.

It appears that the term "mutation" has also acquired an unfortunate connotation of undesirableness, products being considered aberrants (or deviation from normal). To some

extent, this prejudice does have some legitimate basis in the sense that the most visible mutations in many crop species either are deleterious or if not, carry with them some undesirable pleiotropic effects (in practise, pleiotropy and extremely tight genetic linkage are difficult to distinguish). The reports on the frequency of desirable mutations in potato are conflicting. For example, Asseyeva and Yashina (1968) concluded that only 6 or 200 induced mutations they examined in potato had some practical value and of the 6, only one was found in a commercial cultivar. On the other hand, Solomko (1962; 1965) claimed that only 4 - 8% of induced changes obtained are adverse types. Even 17% of mutants produced in some well known Russian cultivars were reported to be useful, some of which were suitable for direct practical use. Van Harten (1978) surmised that the effect of pleiotropism is less important than anticipated before and assuming that high quantities of mutations can be induced, types without negative side-effects undoubtedly can be found.

The other reason for the lack of success in applying mutation breeding is the tendency of many mutation breeding experiments to dwell on rather preliminary trial stages (Van Harten, 1978). Many experiments were on limited scale and only for a few vegetative generations. In some cases, it is difficult to determine, especially when work was conducted with very limited vegetative generations, whether the reported mutation is real or due to primary injury or physiological damage incurred by mutagenic agents. Non-hereditary effects should be ideally set apart from hereditary changes. In mutation experiments, only healthy and virus-free plant materials (virus symptoms have often been mistaken for mutation) should be used and this point has been neglected by many investigators.

Ideally, mutations of a non-chimeric nature, i.e., 100% solid mutation, is highly preferable in breeding. With vegetatively propagated species such as potato, the multi-layered structure of the shoot apex and of tissues derived from it enhance the development of a single cell mutation into a more or less stable periclinal chimera (Jorgensen and Crane, 1972). Chimeric plants are those composed of both mutated and non-mutated somatic cells or tissues. Depending upon which histogenic layer these mutated cells occur, they may or may not be possible to regenerate. Only mutations that are possible to regenerate are useful in breeding. For example, some bud sports cannot be reproduced generatively (by seed) because the mutation occured in cell layers other than the subepidermal zone (L II cell layer). Dorst (1924) as cited by Van Harten (1978) mentioned that only mutations present in the subepidermal layer can be propagated generatively since germ cells arise only from this zone.

A method to produce high frequencies of solid mutants has been developed (Van Harten *et al*, 1972). The method employs tuber-eye plugs from which the main eyes have been removed before irradiation with high doses and dose rates. The sprouts arising from the eye region after irradiation are dissected and planted out individually. The sprouts which develop about three months after radiation treatment are mostly of adventitious origin, producing mutants which are practically 100% solid. This technique to produce chimera-free mutations is rather laborious however and it seems necessary to look for a better and quicker method (Van Harten, 1978).

Taking into account the favorable developments in mutation techniques, as well as the fact that massive, laborious conventional breeding programs do not always lead to success, Van Harten (1978) argued conceptually that mutation breeding does have a role to play in potato improvement. He cautioned however that realism must be exercised in applying mutation technique as a practical breeding tool. As long as sufficient genetic variation can be obtained more easily (such as with conventional breeding), the mutation breeding method should not be applied. The most promising approach, in Van Harten's view, is to apply the

mutation method in advanced stages of conventional breeding to cure certain, well-defined "defects" in promising breeding materials and in commonly grown cultivars.

5.2.3 Other interesting developments in the field

Potential of monohaploids

The successful derivation of dihaploids from cultivated tetraploids has its logical extension in further attempts to reduce the ploidy to monoploid (monohaploid) level. There are certain genetic and breeding implications to this approach. Of most immediate significance to the breeder is the possibility of generating completely homozygous diploids. Their use in developing potato hybrid varieties reproducible as true seeds, along the line of hybrid maize, would be a breakthrough in potato breeding with far-reaching impact (see further discussions below).

Two lines of approach have been tried in generating monohaploids of potato. The first is an extension of the parthenogenetic method used originally to derive dihaploids. Breukelen *et al* , (1975; 1977) successfully produced 85 viable parthenogenetic monohaploids (2n = 12) from *S. tuberosum* and *S. verrucosum.* All were induced using diploid *S. phureja* clones homozygous for the genetic marker, embryo spot, as pollinator. The frequency of monohaploid induction was consistent for three successive years—14,17, and 17 per 100 berries. Although none of the monohaploid plants showed male or female fertility, doubling of their chromosome number by colchicine yielded homozygous diploids with low pollen quality but good seed fertility. Other species, e.g., *S. multidissectum* and *S. berthaultii*, yielded no monohaploids suggesting that highly self-incompatible species may have accumulated more lethal genes concealed in the heterozygous condition. Of the three species tested, only *S. verrucosum* is self-compatible.

Monohaploid plants have also been produced by inducing plantlet formation in anther cultures (Foroughi-Wehr *et al* , 1977; Sopory *et al* , 1978; Weatherhead and Henshaw, 1979). Plantlets derived from anther cultures were a mixture of polyploids, dihaploids and monohaploids, majority of which are non-haploids (Foroughi-Wehr *et al* , 1977) which is often expected when plantlet regeneration occurs via calluses (Sopory *et al* , 1978). Jacobsen and Sopory (1978) observed that the genotype of the clone, apart from physical-chemical factors, is very important in the success of anther culture and that improvements may be made by selecting and recombining existing genotypes to develop clones with positive response to anther culture.

Foroughi-Wehr *et al* (1977) claimed that anther culture has the advantage over female parthenogenesis (Breukelen *et al* , 1975; 1977) in generating monohaploids on grounds that there are thousands more pollen grains than there are ovules. However, they failed to mention that dihaploid potatoes often have poor pollen fertility thus negating its advantage in number. Moreover, chimeric plantlets appear occasionally from anther culture. Plantlets from anther culture of cultivated potato have also proven to be difficult to obtain (Irikura amd Sakaguchi, 1972; Irikura, 1975). On balance then, it would appear that the female parthenogenetic method has more merit than the anther culture technique, besides being comparatively simple. However, anther culture techniques have greatly advanced that more dihaploid plantlets can now be generated (Wenzel and Melchers, 1979).

Three possible methods (Breukelen *et al* , 1977) have been suggested to double the chromosome number of monohaploids to produce homozygous diploids—via the use of colchicine, by unreduced (2n) gametes, and by protoplast fusion. Of these, the use of

colchicine is well known and needs no further elaboration. Unreduced gametes appear frequently in potatoes and may have even played a very important role in the polyploid evolution of some species (Hawkes, 1978). Protoplast fusion, on the other hand, is relatively unexplored field but advances are steadily coming.

Protoplast fusion

Protoplast fusion is essentially somatic hybridization where the intact genomes and cytoplasms of different parents are induced to fuse via their protoplasts. Interest in the field is high because of the potential for wide somatic cell fusion between distantly related plants (Nickell and Heinz, 1972). Thus far, plantlets have been successfully generated from fused proptoplasts of some plant species and fusion without regeneration on a number of others. For examples, Carlson *et al* , (1972b) isolated protoplasts of *Nicotiana glauca* and *Nicotiana langsdorfii,* fused them and isolated somatic hybrid plants by means of a selective screen system that depended on differential growth of the hybrid on a defined media. Plantlets from fused protoplasts of carrots have also been produced (cf. Nickell and Heinz, 1972).

In potato, successful regeneration of plantlets from isolated mesophyll protoplasts was reported by Binding *et al* (1978) and Grun and Chu (1978). Protoplasts from 4 of 6 dihaploid *S. tuberosum* clones regenerated into plants which had stable karyotype (Binding *et al* , 1978). Melchers *et al* (1978) regenerated somatic hybrid plants of potato and tomato from fused protoplasts. Four regenerated plants showed expression of both tomato and potato nuclear genes proving these plants to be somatic hybrids. The chilling resistance of these somatic hybrids was invesitgated by Smilie *et al* (1979). Tomato is generally susceptible to chilling temperatures whereas potato is relatively resistant. The study showed that chilling resistance of somatic hybrids was intermediate between tomato and potato, prompting the above investigators to conclude that somatic hybrids may be very useful to transfer the chilling resistance of potato to tomato.

Somaclonal variation

The potential of variation between plants generated from single cell cultures of potato has also been explored in the manner that had been done for sugar cane (Heinz, 1977 cf. Shepard, 1980) or in tobacco (Carlson *et al* , 1972a). Wenzel and Mechers (1979) cited that microspore and protoplast culture techniques to derive plantlets from *S. tuberosum* dihaploids are vastly improved—more than 2,000 microspore-derived and several hundred protoplast-derived plantlets have already been produced in their program. They proposed an extension of Chase's (1963) analytical synthetic breeding scheme whereby tetraploids are reduced to dihaploids via female parthenogenesis (using *S. phureja* pollinators); selected dihaploids carrying complementing traits are then further reduced to monohaploids with selection for appropriate traits and subsequent *in vitro* chromosome doubling; two complementing doubled monohaploids (dihaploids) are then crossed to produce diploid clones carrying the traits of both parents, after which fusion of their protoplasts is carried to create the synthetic, heterozygous tetraploids carrying all the desired characters of the four original tetraploids clones.

Shepard et al (1980) reported that clonal populations regenerated from single leaf cell protoplasts on potato cultivar Russet Burbank displayed a high frequency of variation for several horticultural and disease resistance characters. Observation over a period of three tuber generations suggested stable changes in tuber shape, yield, maturity, photoperiod requirement for flowering and plant morphology. Enhanced resistance to early blight and late

blight also regularly occurred within the regenerated populations. While the results obtained were unquestionably impressive, there were some unsettled questions, e.g. source of protoclonal (protoplast-derived clones) variation without mutagenesis—epigenetic causes, somatic mutations, or point mutations in leaf cells? It has been argued however that vegetatively propagated crops do exhibit a high degree of spontaneous somatic variation such as for example in sweet potato cultivar Centennial where two plants in 100 have been estimated to be morphologically distinct.

True potato seed for commercial production

Commercial planting of potatoes from true (botanical) seeds in place of tubers is another area of development with major implications especially for developing countries without an effective, well-organized tuber seed programs. Traditionally, raising potatoes from the true seeds is restricted mainly to the first generation after hybridization; thereafter, selected plants and established varieties are propagated by tubers. Without an effective tuber multiplication scheme, clones invariably accumulate degenerative viral diseases that significantly cause yield losses. It is probably fair to conclude that low yields of potatoes in developing countries, where lack of good seed program is more of a rule than exception, are in large part due to the use of poor, virus-infected seeds.

True potato seeds (TPS), on the other hand, are almost completely virus-free (spindle-tuber viroid is an exception since it is seed-transmissible according to Diener, 1971). Apart from the advantage in health of planting materials, growing commercial crops from TPS offer other benefits (Bedi, 1978) such as: use of TPS can reduce volume and weight of planting materials, e.g., 65 grams of TPS can plant a hectare that would require 2 tons of tubers; TPS retains viability without serious deterioration of vigor and viability (Howard, 1969; 1975; 1978; Simmonds, 1968); TPS can be stored at room temperature without physiological impairment (Howard, 1978) while tubers need carefully controlled, expensive cold store facilities; TPS can substantially reduce production cost as they are easier and cheaper to produce, light in weight thus cutting transportation and storage costs; TPS would free a major portion of land devoted to seed potato crops for production of other food crops. All in all, it is clear that TPS carries overwhelming advantages over tuber seeds. The negative points of TPS are purely technical and, with research efforts being now intensified in many parts of the world, may possibly be resolved in time.

The most obvious disadvantage of TPS is the lack of phenotypic uniformity for many characters, e.g. seedling vigor and emergence; tuber attributes such as shape, color, size, depth of eyes, etc., maturity, general vegetative growth; and even consistency in yield performance from plant to plant. Admittedly, one can argue that the requirements for phenotypic uniformity in developing countries are not as rigid as in areas of the world where potato is a major crop. However, a certain degree of yield stability from plant to plant would be desirable. A wide range of maturity of TPS could significantly alter the cropping system in place and may pose some problems. Small farm systems where multiple, sequential croppings are practised would not be favorable for TPS production because of variable and long maturity. The more visible criteria of uniformity (those relating to external tuber appearance) are without doubt the easiest to resolve from a breeding standpoint.

The genetic basis of TPS variability lies on the high level of heterozygosity in tetraploid clones. Regardless of whether TPS are derived from hybridization, selfing, or open-pollination, variability will always be released and will be evident among progenies. Apart from its heterogeneity the overall performance of TPS may not compare with tuber

propagation, e.g. smaller yield on per plant basis, smaller tuber size, fewer tubers, longer maturity, etc. Selection for important TPS traits appears possible however and evidence points to an expected rapid improvement in many of these characters (Anon, 1980b). For example, in an experiment using North Carolina Design I developed from 15 randomly selected male clones each crossed to a random sample of four female cones (all clones were derived from a Neo-tuberosum population), additive genetic variance was significant for 10 of 16 traits studied (Table 9). Yield was not considered because of its non-additive nature in the population sampled.

Table 9. Narrow sense heritability (h^2) estimates from full-sib families of several traits in potatoes propagated by TPS (after Anon, 1980)

Character	Heritability
Germination percentage	.53
Transplant survival	.30
Nursery vigor	.56
Nursery uniformity	.33
Resistance to Rhizoctonia	.55
Days to maturity	.57
Number of berries	.58
Tuber number	.60
Tuber size	.79
Depth of eyes	.57

High yield *per se* appears to be obtainable in TPS. In an experiment comparing F_1 hybrid seedlings, open-pollinated (OP) seedlings and F_1 tuber-propagated families, F_1 seedlings and F_1 tuber-propagated entries significantly outyielded the OP seedlings in one of two locations (Anon, 1980b). No significant differences were noted in another test site. F_1 and OP seedlings tended to produce smaller tubers than F_1 tuber-propagated plants. This result was explained on the basis that seedlings usually produced a large number of secondary stems by profuse branching. Selection for large tuber size of TPS should be achievable however in view of its fairly high heritability (see Table 9). Certain agronomic management such as controlling the number of branches/stems by pruning could also possibly improve the size of tuber sets in TPS. This practise is not new—Taiwanese farmers regulate stem density of commercial tuber—propagated potatoes to produce uniform, good size tubers (personal observations).

In another study, Bedi (1978) reported that one TPS line approached the yield of commercial varieties raised by normal vegetative means. Accatino (1980) observed the presence of several hybrid progenies with good yielding ability and good uniformity of tuber color and shape in a growth duration of 90 days at San Ramon, and Lima, Peru. Yields of 15-26 tons per hectare have been noted among a broad sample of TPS families (Anon, 1980b). Fifteen families were also found to be very uniform.

When the subject of high yield combined with agronomic uniformity comes to light, breeders cannot help but be reminded of the classical example of success with hybrid maize. There is no doubt that potato, being genetically an outbreeder, is highly heterozygous and exhibits significant heterosis (Rothacker, 1962; Glendenning, 1969; Cubillos and Plaisted,

1976; Tarn and Tai, 1977). Therefore, high yield through maximization of heterosis is a logical objective in TPS cultivars. The problem lies in achieving agronomic uniformity. In maize, homogeneity is achieved in the hybrids because essentially homozygous inbred parents are used in creating the hybrids. However, potato is a highly heterozygous tetraploid and any attempt to inbred clones as suggested by Krantz (1946) will be time-consuming since the approach to homozygosity is slower than in diploid crop species like maize. Moreover, few Tuberosum varieties are pollen-fertile; hence inbreeding by selfing restricts the number of inbred lines of diverse origins that can be produced (Howard, 1970).

The producion of dihaploids (see Section 5.2.1) and monohaploids (discussed earlier in the current section) provides a serious alternative to inbreeding at the tetraploid level. At the dihaploid level, De Jong and Rowe (1971) concluded that obtaining homozygous clones appears possible. The advantage of inbreeding at the diploid level in terms of a faster approach to homozygosity is clear. Assuming no selection for heterozygosity, the diploid S_5 generation is about 97% homozygous. By comparison, the same generation in an autotetraploid assuming random chromosome segregation is only 57% homozygous (Bartlett and Haldane, 1934). Krantz (1946) considered potato as an autotetraploid because its actual yield depression as percent of mean F_1 yield was lower than those calculated on the assumption that potatoes are allotetraploids.

Apparent homozygosity in diploids has reportedly been achieved via monohaploid induction followed by colchicine doubling (Breukelen *et al,* 1975; 1977). Wenzel and Melchers (1979) also cited the rapid advances that have been achieved in anther and protoplast culture techniques. In time, therefore, generating homozygous clones, be they diploids or tetraploids, should be within reach of potato breeders. The limitation appears to be in finding homozygous clones with improved male and female fertility so that they can be used in creating reproducible F_1 or open-pollinatd TPS cultivars. There are some indications that intercrosses among dihaploid clones or hybridization with cultivated diploid species can alleviate the fertility and vigor problems (Ross *et al,* 1964; Hougas and Peloquin, 1965; Rowe, 1967a). If this is so, producing TPS hybrids may necessitate parental stock development to improve vigor and attain high seed productivity. Careful selection of parents must be done however to insure that recovery of vigor and fertility is not done at the expense of relative agronomic uniformity.

Assuming that homozygous, good-combining diploid stocks with high fertility can be produced and a regular tetraploid TPS hybrid is desired, some limitations of the approach should be taken into account. Chromosome doubling of homozygous diploids will not alter its inbreeding coefficient (F = 0) but putting two doubled stocks into hybrids, each with F = 0, will result in progenies partially retaining some of the inbreeding of the parents (F = 1/3 among progenies). Thus, loss of vigor in the hybrid progenies is theoretically expected. A mechanism that might be exploited to achieve high yield and agronomic uniformity of TPS at the tetraploid level is through the sexual polyploidization process (via 2n or unreduced gametes fromed by FDR, or first division restitution). Mendiburu and Peloquin (1971) observed that the tetraploid progenies from 4x-2x matings are not only vigorous and high yielding but also uniform. Similar results were obtained by De Jong and Tai (1977; 1978). The cytological basis of 2n pollen formation which leads specifically to heterotic tetraploid progenies in 4x-2x or 2x-2x crosses, i.e., FDR through parallel spindle formation during meiosis, is simply inherited (Mok and Peloquin, 1975a; 1975b) and manifested in the pollen phenotype (Simon and Peloquin, 1976) so that it can easily be bred into dihaploid stocks. If diploid clones with good agronomic attributes, high frequency of 2n gamete formation via

FDR, and good combining ability can be found, then production of relatively uniform, high yielding TPS (with mostly tetraploid progenies) may possibly be achieved.

Summary

A review of breeding and genetics of potato has been presented here to provide the breeders in developing countries with some fundamental guidelines in potato breeding and an updated knowledge of recent developments in the field.

The survey of published articles was made as comprehensively as possible but, understandably, other important studies may have been inadvertently omitted. Part of the difficulty lies in the long history of potato as a scientific subject, a good indication of its great importance. Most of the different subjects dealt with in this chapter are replete with volumes of literature so that omission of a number of them was inevitable.

It must be mentioned that the potato breeding problems in developing countries obviously transgress those that were cited and/or implied in the present article. However, emphasis was placed only on the most common ones for the sake of giving them a slightly more comprehensive treatment.

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