

Breeding Potatoes for Long-day, Temperate Climates

T. R. Tarn, G. C. C. Tai, H. De Jong,
A. M. Murphy, and J. E. A. Seabrook*

Research Station, Research Branch, Agriculture Canada
P.O. Box 20280
Fredericton, N.B. E3B 4Z7, Canada

I. Introduction	218
II. Germplasm	219
A. The Germplasm Resource	219
B. Reproduction Biology	223
C. Germplasm Improvement	227
D. Strategies for Germplasm Utilization	229
III. Cultivar Development	233
A. The Breeding Plan	233
B. Choosing Parents and Crosses	236
C. Early Generation Selection	241
D. Late Generation Selection	244
E. Evaluation of Advanced Selections	246
IV. Production Traits	248
A. The Ideotype	248
B. Plant Architecture	249
C. Breeding Implications	250
V. Utilization Traits	252
A. Nutritional Traits	252
B. Glycoalkaloids	254
C. Fresh Consumption Traits	255
D. Processing Traits	258
E. Tuber Defects	260
F. Breeding Implications	262
VI. Protection Traits	264
A. Resistances to Diseases and Pests	264
B. Bacterial Diseases	270
C. Fungal Diseases	272
D. Viral Diseases	276
E. Insects	280
F. Nematodes	283
G. Herbicide Resistance/Tolerance	285
H. Gaseous Pollution Sensitivity	286

*The authors have received support from many people during the preparation of this review and wish to acknowledge specially the assistance of the Fredericton Research Station librarian, Mr. Richard Anderson.

VII.	In Vitro Traits	286
	A. Regeneration	287
	B. Maintenance of Disease-causing Organisms	288
	C. Apomixis	288
VIII.	Cultivar Release	288
	A. Distinctness	289
	B. Uniformity and Stability	289
	C. Availability of Seedstock	291
	D. Management Profiles	291
IX.	Summary	292
	Literature Cited	293

I. INTRODUCTION

The potato is one of the world's major food crops, ranking fourth in production after rice, wheat, and maize (Ross 1986) and being produced in 126 countries (Burton 1989). Since the crop has spread from the Andes of Peru and Bolivia it has been selected for adaptation to a wide range of environments and is now grown in most regions of the world. The scope of this review is limited to breeding for long-day, temperate climates, particularly those of North America, Europe, southern Australia, and southern South America. To consider just two of these regions, Pavek (1987) reports 22 breeding programs in Canada and the USA, and Świeżyński (1987) reports 321 breeders in 23 European countries. Together these 25 countries produce about 12 million first year seedlings annually. Issues related to breeding for tropical environments, including a different group of diseases and pests, and management with True Potato Seed technology are not covered in this review (for current work see CIP 1985; Malagamba and Monares 1988).

The biology of the potato—a crop in which new cultivars are generally produced by cross pollination and then propagated vegetatively—has resulted in the development of principles and practices in cultivar development that are distinct from those of most other major crops. The most comprehensive recent review of potato breeding is that of Ross (1986). Overviews of European and North American programs are provided by Świeżyński (1987) and Pavek (1987), respectively, while other reviews, including Erjefält (1986), Genet and Anderson (1985), Hoopes and Plaisted (1987), and Mackay (1987), focus on specific programs. Three symposia proceedings (Beekman et al. 1986; Jellis and Richardson 1987; Louwes et al. 1989) also cover potato breeding.

This review brings a North American perspective to potato breeding and genetics. It reflects the philosophy of the Agriculture Canada potato breeding program at Fredericton where physiology and crop development are stressed. Germplasm utilization and research on breeding and

selection methods are reviewed, and crop development is considered from a breeding perspective. Eighteen traits related to fresh and processing uses are specifically reviewed, as are resistances to 17 pathogens and six pests. A short section deals with in vitro traits and progress in various areas of biotechnology is included. This review is intended as a reference for those working in potato genetics and breeding, as well as those working on the edge of these disciplines or new to the crop.

II. GERMPLASM

A. The Germplasm Resource

1. Species diversity and distribution. The cultivated potato, the wild tuber-bearing species, and their allies belong to the section *Petota* Dumortier in the subgenus *Potatoe* (G. Don) D'Arcy of the genus *Solanum* L. (D'Arcy 1972). Species in section *Petota* are characterized by actinomorphic flowers, a jointed or articulated pedicel or flower stalk, unbranched glandular or eglandular hairs, no thorns or spines, and generally compound leaves. Some 200 species are involved in this grouping (Huamán and Ross 1985), and they have been variously divided by different authors into a number of groups or series. The most frequently followed system of classification has been that of Hawkes (1982). Hawkes (1990) has now proposed a new classification in which the 18 old series in section *Petota* have been divided into subsections. Subsection *Estolonifera* Hawkes contains two series of non tuber-bearing species, and subsection *Potatoe* G. Don contains 19 series of tuber-bearing species.

A conventional classification is followed by all workers for the wild potato species, but the cultivated species are treated differently by different authors. Hawkes (1990) recognizes three diploid species, two triploid species, the tetraploid *S. tuberosum* L. with subspecies *tuberosum* and *andigena* Hawkes, and a pentaploid species. On the basis of a common heritage for all but two of these species, Dodds (1962) proposed to include all except a triploid and a pentaploid under the name *S. tuberosum* L., within which he recognized further subdivisions by ploidy and Group. This system has been adopted by many of those working with the primitive cultivated potatoes. The systems are compared in Table 8.1.

The potato encompasses an extremely wide range of diversity that is reflected in morphology, physiological adaptation, and responses to

Table 8.1. Comparative classifications of cultivated potatoes (after Dodds 1962).

Species and Groups (Dodds 1962)		Ploidy	Species (Hawkes 1990)
<i>S. tuberosum</i> L.	Stenotomum	2x	<i>S. ajanhuiri</i> Juz. et Buk.
		2x	<i>S. stenotomum</i> Juz. et Buk.
	Phureja	2x	<i>S. phureja</i> Juz. et Buk.
	Chaucha	3x	<i>S. chaucha</i> Juz. et Buk.
	Andigena	4x	<i>S. tuberosum</i> L. ssp. <i>andigena</i> Hawkes
	Tuberosum	4x	<i>S. tuberosum</i> L. ssp. <i>tuberosum</i>
<i>S. juzepczukii</i> Buk.		3x	<i>S. juzepczukii</i> Buk.
<i>S. curtilobum</i> Juz. et Buk.		5x	<i>S. curtilobum</i> Juz. et Buk.

pests and pathogens (Hanneman 1989). A valuable guide to describing the morphological diversity is the descriptor list produced by the International Potato Centre and endorsed by the International Board for Plant Genetic Resources (Huamán et al. 1977). Of the 176 species for which chromosome counts are recorded, 73% are diploid, 15% are tetraploid, and 6% are hexaploid (Hawkes 1990). The balance are hybrid species that are triploid or pentaploid.

These potatoes are distributed from Colorado and Nebraska, USA (41°N) in the north to the islands off Chile (45°S) in the south, and from the Pacific coast of Peru to the Atlantic coast of southern Brazil and Uruguay. They occur from relatively low altitudes at the north and south limits of their range up to 4600 m in the Andes mountains in tropical latitudes. While the environments in which they grow are extremely variable with regard to ranges of temperature, precipitation, and light intensity, most species occur in more or less temperate environments. The species also have in common a relatively short-day growing season—almost 75% of the species occur within tropical latitudes—and they almost all have a rest season in which the tubers remain dormant through a period of drought or low temperature stress. Habitats are described in detail in several monographs (Correll 1962; Ochoa 1962; Hawkes and Hjerting 1969; Hawkes and Hjerting 1989).

The accepted evolutionary relationships of the potato species were established on the basis of cytogenetic studies (Hawkes 1982) and have been supported by most other experimental investigations including the chloroplast DNA studies of Hosaka et al. (1984). The potato is postulated to have originated in Mexico in the late Cretaceous to Tertiary times resulting in the modern group of morphologically diverse and cytogenetically isolated group of Mexican diploid species (Hawkes 1990). In the early Pliocene, southward migration of these early diploids led to the evolution of the diploid species that are now widespread in the Andes. Subsequently, it is proposed that two waves of return migrations

led to the formation of the Mexican tetraploid and hexaploid species. In the Andes, domestication of the potato produced the primitive cultivated species. In these ways the potatoes have evolved so that the cultivated species have retained cross compatibility with most of the South American diploid species and the Mexican polyploid species, leaving isolated only the Mexican diploids and several South American species.

Archaeological evidence suggests that the potato has been in cultivation in Peru for at least 10,000 years (Ugent et al. 1982), while evidence in Chile dates taxonomically different material in cultivation 13,000 years ago (Ugent et al. 1987). The search for the putative parents of the cultivated potato has involved a wide range of experimental approaches including cytogenetics and morphology (Cribb and Hawkes 1986), cytoplasmic sterilities (Grun 1979), allozyme variation (Oliver and Martínez Zapater 1984), and chloroplast DNA (Hosaka 1986). The increasing evidence for intraspecific diversity (Hosaka and Hanneman 1988) suggests that the cultivated potatoes may have originated more than once.

2. Gene banks. The International Board for Plant Genetic Resources lists collections of potato species and cultivars in 42 countries (Lawrence et al. 1986), of which seven may be considered major world collections (Hermesen 1989). Several additional countries within the distribution area of the potato species also maintain valuable collections of their native species. Although the documentation of such germplasm collections is improving with the adoption of computerized data bases, only two of the collections have published up-to-date inventories. These are the German-Netherlands Potato Genebank in Braunschweig, Germany (Hoekstra and Seidewitz 1987), and the USA Inter-regional Potato Introduction Project, Wisconsin (Hanneman and Bamberg 1986). Such documentation is essential to the effective use of these collections. Systematic evaluation is a part of germplasm collection activities only at the International Potato Center, the German-Netherlands Potato Genebank, and the USA Inter-regional Potato Introduction Project (Hermesen 1989). The evaluation procedures have been described in detail for the German-Netherlands collection (Van Soest 1983b) and for the USA collection (Hanneman 1989). Evaluation data have been published with inventories only for the German-Netherlands and the USA collections (Hanneman and Bamberg 1986; Hoekstra and Seidewitz 1987).

3. Exploration and collection. The major potato germplasm collections contain in the living state most of the species described. Some species are very well represented—these are generally the widespread and vigorous growing ones such as *S. acaule* Bitt., *S. chacoense* Bitt., *S. demissum*

Lindl., *S. gourlayi* Hawkes, and *S. stoloniferum* Schlechtd. & Bché. However, parts of distribution areas may be poorly sampled, entire species inadequately sampled or even absent, or potato species habitats threatened. Priorities for continuing germplasm collection were recommended at an International Potato Center planning conference in 1979 (CIP 1979).

The reporting of the results of collecting expeditions is becoming common (Van Soest et al. 1983a; Okada and Clausen 1984; Tarn et al. 1985; Spooner et al. 1991). This should speed up the documentation and evaluation of new accessions and facilitate the planning of future work of this kind.

4. Germplasm maintenance. The nature of the potato allows germplasm to be maintained as true seed or as clones depending on the situation. Systems for the maintenance of true seed need to be designed to minimize the frequency of renewal and to protect against genetic drift. Both Lange (1976) and Hanneman (1989) described procedures for seed increase in greenhouse environments. In both cases they grow out 20 plants of each accession. Van Soest (1983a) has also found increases of self-incompatible species to be easy and reliable when carried out in the field. Following seed increases it is necessary to grow out samples to ensure that mixtures have not taken place. Seed is best maintained at reduced moisture content, and stored in moisture-proof metalized polyester packets at 1–3°C temperatures. High viability can be retained for at least 28 years (Towill 1983). Potato seeds have been shown to survive liquid nitrogen storage (Towill 1982), and low temperature storage may be a practical procedure.

The maintenance of potato clones presents more problems and more options. Field or greenhouse maintenance is becoming the least preferred choice because of the risk of virus or viroid infection, and because of the accumulation of tuber-borne diseases on the seed pieces.

5. Storage of potato accessions in vitro. The upkeep of an in vitro germplasm collection can be reduced by changing the cultural conditions. Thus, maintaining potato material in culture for long periods of time involves slowing growth so that transfers are not as frequent (Lizarraga et al. 1989).

Lowering the temperature from a normal of 18–22°C to approximately 6°C reduces the period between sub-cultures. Care has to be taken not to unduly stress the tissues (Dodds 1988). It is possible that potato cultures maintained under minimal growth conditions could be subject to genetic change just as true seeds in long-term storage are affected (Dourado and Roberts 1984). Growth retardants in the culture medium have been

extensively used in germplasm collections of potato (Mix 1985; Lizaraga et al. 1989).

Cryopreservation of potato material is possible (Bajaj 1981, 1986; Towill 1984; Henshaw et al. 1985), but the technology does not yet appear to have been developed for research and breeders' germplasm collections (Dodds 1988). Novel systems of long-term conservation for potato such as serial microtuber production have been proposed (Kwiatkowski et al. 1988).

6. Quarantine. Germplasm exchange is essential to share the benefits of native species, highly selected cultivars, and a wide variety of lines selected for research purposes. In potato the exchange of clonal material has long been through the distribution of tubers with the associated risk of spreading a large number of diseases (Fry 1982) and pests. The development of plant quarantine measures has provided regulatory infrastructures to prevent the spread of dangerous or potentially dangerous pests and diseases (Mathys and Baker 1980), and the widespread adoption of virus-tested material and procedures for the *in vitro* distribution of clones (Seabrook and Coleman 1988) has done much to reduce the risks. Extensive testing for disease is necessary for imported material.

While this solves most problems related to the exchange of vegetative material, most species material is distributed as true seed. Since four viruses (Jones 1984) and potato spindle tuber viroid (Salazar 1989) are seed-borne, the risk of further spread of these pathogens remains. Extensive testing is still necessary as virus and viroid diseases can be transmitted *in vitro* (Singh et al. 1988).

B. Reproduction Biology

1. Physiology of flowering. Since the cultivated potato is primarily reproduced asexually, there is a limited amount of research data on the flowering process. In general, flowering is influenced by the photoperiod, light intensity, temperature, and genotype. Relatively long days, high light intensity, and moderately high night temperatures tend to stimulate flower bud initiation and flower development (Levy and Kedar 1985; Haynes and Haynes 1988; Turner and Ewing 1988). Most wild potato species and many cultivated potatoes flower profusely under a considerable range of environmental conditions. On the other hand, some cultivars flower only sparsely and in such cases the control of environmental factors is critical.

2. Hybridization. Under natural conditions, potatoes are pollinated

primarily by wild bees, especially bumble bees. Pollen seems to be the primary factor which attracts bees to potato flowers; male sterile plants are seldom visited by bees (Sanford and Hanneman Jr. 1981; White 1983). Both self-compatible and self-incompatible species are dependent on bees for pollination (Glendinning 1976; Camadro and Peloquin 1982). Plaisted (1980) has described the hybridization techniques which are commonly used in potato breeding programs. Various chemicals can be used as an aid in hybridization. Gibberellic acid has been used widely to induce and enhance flowering (Zafar 1955; Fischnich and Krug 1959; Pushkarnath and Chauhan 1964a; Ross et al. 1980; Lozoya-Saldaña and Miranda-Velázquez 1987; Hoekstra 1989). Flower retention after pollination can be improved by the use of 2,4-D (Zafar 1955; Dionne 1958). This is particularly useful in crosses which produce too few seeds per fruit to stimulate growth of the ovary (Dionne 1958). Flower retention can also be improved by the application of ethylene inhibitors such as silver thiosulfate (Hoekstra 1989; Rahimi and Carter 1989). Positive results with flower retention have also been reported with Gapol, a mixture of several growth regulators commonly used for flower retention and fruit set (Lozoya-Saldaña and Miranda-Velázquez 1987). The histology of floral abscission in the potato has been described by Pushkarnath and Chauhan (1964b).

3. Sterility. There are many types of male sterilities. These are often caused by an unfavorable reaction between the cytoplasmic sterility factors of *S. tuberosum* Group Tuberosum that are transmitted through the seed parents and the usually dominant chromosomal genes of wild or primitive cultivated species (Howard 1970; Grun 1979; Ross 1986; Amoah and Grun 1988; Kaul 1988). Restorer genes for genetic-cytoplasmic male sterility have been reported (Peloquin and Iwanaga 1981). Expression of such restorer genes can be improved by selection for adaptation (Vilaró et al. 1989). Genetic male sterilities apparently independent of cytoplasmic factors have also been reported (Birhman and Kaul 1989a). Little is known about female sterility, but considerable genetic variability exists among cultivars.

Few interspecific hybrids are sterile because of the failure of chromosome pairing. The chromosomes of different genomes of tuber-bearing *Solanum* species are not structurally differentiated to the extent that it results in the failure of chromosome pairing at meiosis (Ramanna and Hermesen 1979). However, such sterilities do occur in hybrids between non tuber-bearing and tuber-bearing *Solanum* species (Ramanna and Hermesen 1982). Such sterilities can, to a considerable extent, be overcome by the manipulation of Endosperm Balance Numbers (Section II. B. 5), ploidy level (Section II. B. 6), and bridging crosses (Section II. C. 4).

4. Incompatibility. The primary incompatibility system among the tuber-bearing *Solanum* species is gametophytic and conforms with the one locus *Nicotiana* scheme of oppositional S-alleles (Howard 1970; Hermesen and Sawicka 1979). A two-loci gametophytic system has been found in a number of Mexican species (Pandey 1962a, 1962b) and in the cultivated diploid Groups Phureja and Stenotomum (Abdalla and Hermesen 1971). Most diploid species are self-incompatible, but some Mexican diploid species are self-compatible. Other self-incompatible species may contain some self-compatible genotypes (Hermesen and Sawicka 1979). Self-compatible cultivated diploid hybrids have been used in inbreeding and genetic studies (De Jong and Rowe 1972). Self-compatibility in Group Tuberosum haploids can result from the presence of a translocated S-bearing chromosome fragment (Hermesen et al. 1978). Self-compatibility and abnormal S-gene behavior has been induced in the normally self-incompatible diploid species *S. chacoense* by doubling the ploidy level from monoploid to diploid (Cappadocia et al. 1986).

Most tuber-bearing *Solanum* species are cross-compatible, but both unilateral and bilateral cross-incompatibilities exist. These interspecific incompatibility relationships are still not well understood. In order to distinguish such relationships from the self-incompatibility system as described above, the term incongruity has been applied (Hermesen and Sawicka 1979). The site of the interspecific incompatibility reaction is frequently in the style (Camadro and Peloquin 1981; Fritz and Hanneman 1989).

5. Endosperm balance numbers. Most South American diploid tuber-bearing *Solanum* species can be readily intercrossed. However, some difficulties have been encountered, particularly with several Mexican species. In several compatible interspecific crosses, the hybrid endosperm is known to abort. The endosperm balance number (EBN) concept has been proposed as an explanation for the success or failure of both interspecific and interploidy crosses (Johnston et al. 1980; Johnston and Hanneman 1982). Successful crosses are dependent on normal endosperm development which in turn is dependent on a 2:1 ratio of maternal:paternal chromosomes. Under the EBN hypothesis each species has a genome specific "effective ploidy" or EBN with respect to endosperm function. It is the EBN (not necessarily the ploidy levels) that must be in a 2 maternal:1 paternal ratio for normal endosperm development. EBNs are assigned to each species by crossing to a species used as a standard: the EBN may be different for species of the same ploidy, and species of different ploidies may have the same EBN (Table 8.2). This concept has been used in predicting successful interspecific crosses (Ehlenfeldt and Hanneman 1984; Singh et al. 1990). The EBN itself

Table 8.2. Endosperm balance numbers assigned to entries in the inventory of tuber-bearing *Solanum* species in the Inter-regional Potato Introduction Project, Wisconsin, USA (Hanneman and Bamberg 1986).

Endosperm balance numbers	Number of Species		
	Diploid ($2n = 2x = 24$)	Tetraploid ($2n = 4x = 48$)	Hexaploid ($2n = 6x = 72$)
1	12		
2	42	10	
4		5	7
unknown	30	1	1

appears to be under relatively simple genetic control (Ehlenfeldt and Hanneman 1988).

6. Ploidy manipulations. The cytology of the potato has been reviewed by Howard (1970). This crop offers unique opportunities for ploidy manipulations. Haploids ($2n = 2x = 24$), frequently referred to as dihaploids in European literature, of cultivars ($2n = 4x = 48$) are relatively easy to obtain via parthenogenesis (Hougas and Peloquin 1958; Peloquin et al. 1966; Hermesen and Verdenius 1973; Caligari et al. 1988). They have been used widely in cytogenetic studies, germplasm enhancement, and other breeding-related research (Peloquin 1982; Hermundstad and Peloquin 1985; Peloquin et al. 1989). Haploids and monploids ($2n = x = 12$) can be produced via anther culture (androgenesis). It appears that for the production of haploids, the parthenogenetic method is more efficient than the androgenetic method. However, the androgenetic method appears superior for the production of monploids (Wenzel et al. 1983; Wenzel and Foroughi-Wehr 1984; Powell and Uhrig 1987). Large genotypic differences exist among donor plants for both the androgenetic and parthenogenetic methods of ploidy reduction (see references cited above). By breeding and selection, the efficiency for ploidy reduction via anther culture can be further increased (Uhrig and Salamini 1987).

Sexual polyploidization can be achieved with the use of meiotic mutants. Several such mutants have been discovered and are now being used in germplasm transfer (Peloquin 1982; Peloquin et al. 1989). Diploid mutants which produce gametes with an unreduced chromosome number (commonly referred to as $2n$ gametes in potato breeding literature) are particularly useful in germplasm transfer from the diploid to the tetraploid level. Depending on the cytogenetic mechanism involved in the formation of $2n$ gametes, they can be equivalent to a restitution of either the first (FDR) or the second meiotic division (SDR) (Ramanna 1979; Peloquin 1982, 1983; Veilleux 1985). Sexual polyploidization can involve

the functioning of $2n$ gametes from either or both parents (Mendiburu and Peloquin 1977a). The mechanism of the formation of $2n$ megagametophytes is usually due to the omission of the second meiotic division (SDR) (Jongedijk 1985; Stelly and Peloquin 1986). A series of synaptic mutants allows for a unique combination of meiotic mutants. Although synaptic mutations generally result in a very high degree of sterility, this is not the case when such mutants are combined with mutants such as "parallel spindles" which result in the genetic equivalent of FDR. With FDR, it is estimated that approximately 80% of the heterozygosity of the diploid parent is transmitted to the progeny. A combination of FDR and a synaptic mutant allows for the transmission of 100% of the heterozygosity. Most meiotic mutations in the potato are under simple genetic control (Mok and Peloquin 1975; Peloquin 1982; Jongedijk and Ramanna 1988). Lam (1974) and Ramanna (1979, 1983) disagree with Peloquin (1982) regarding the cytological mechanisms of several meiotic mutants.

Various reports of heterosis resulting from sexual polyploidization (reviewed by Hermundstad and Peloquin 1987) indicate that these methods are superior to the ploidy manipulation by asexual means such as colchicine doubling of the ploidy level. It has been postulated that the heterotic response is the result of inter- and intra-allelic interactions which can occur when $2n$ gametes formed via FDR are involved in the polyploidization (Mendiburu and Peloquin 1977b). Nevertheless, somatic doubling of the ploidy level can be used to develop multiplex polyploid genotypes which in turn can be very valuable for the transfer of simply inherited traits (Toxopeus 1953). There are several methods for the ploidy doubling with colchicine in potato (Ross 1986). Maris (1990) found in a comparison of diploid and tetraploid families derived from *S. phureja* $\times$ *S. tuberosum* haploids and their vegetatively doubled counterparts that the tetraploid level is superior to the diploid level.

More recently, it has become possible to manipulate the ploidy level by protoplast fusion (Ross 1986; Deimling et al. 1988). These techniques can be used to develop interspecific hybrids which may be difficult to produce via sexual methods (Helgeson 1989a). However, protoplast fusion may also lead to somatic variability (Jones 1987) and loss of chromosomes (Puite and Mattheij 1989).

C. Germplasm Improvement

Germplasm improvement or enhancement has been reviewed by Roath (1989). It can be defined as transferring useful genes from exotic or wild types into agronomically acceptable backgrounds. Germplasm improvement does not include cultivar development. The reason for using a

specific germplasm source may, at least in part, determine the approach to its improvement. If the primary role of an unadapted species is as a donor of some specific trait, then the need for a comprehensive improvement program is considerably less than if the germplasm source is expected to serve as a source of added genetic variability for many traits. The latter approach does not have many parallels in other crops. It requires a relatively long-term commitment without immediate pay-off in terms of new varieties (Plaisted and Hoopes 1989). This is probably the major limiting factor in more extensive germplasm utilization in potato breeding programs in North America (Hanneman, personal communication).

1. Adaptation. Most potato species are short-day plants and produce few or no tubers under long-day conditions (Howard 1960; Hermundstad and Peloquin 1985). Group Tuberosum, which was selected from the short-day Group Andigena under the long-day conditions of Western Europe, is generally considered to be day-neutral (Howard 1970; Simmonds 1976; Menzel 1985a, 1985b). The relatively long, cold winters of many potato growing areas require a rather long tuber dormancy in commercial cultivars. Some germplasm sources such as Group Phureja have no dormancy at all (Howard 1960), whereas others may have a long dormancy. Other traits where germplasm sources may differ considerably from commercial cultivars include length of stolons, ease with which tubers detach from the stolon at harvest, stem number, tuber number, tuber size, eye depth, and freedom from glycoalkaloids in the tuber (Simmonds 1969). All of these can be improved by selection. Several methods of germplasm improvement are discussed below.

2. Population breeding. Mendoza (1989) has reviewed population breeding as a tool for germplasm improvement. In the UK Simmonds (1966, 1969) initiated a selection scheme among populations of the South American primitive cultivated tetraploid Group Andigena. After only two cycles of selection (in five years), the resulting long-day adapted Neo-Tuberosum populations were judged to be approximately halfway between Group Andigena and Group Tuberosum. Glendinning (1976, 1979) has continued this work and has established a new broad-based population by crossing Neo-Tuberosum with Group Andigena. In New York, Plaisted (1983) commenced a Group Andigena improvement program based largely on the one initiated by Simmonds. After six cycles of recurrent selection for adaptation, considerable gains in photoperiod adaptation and earliness were reported (Rasco et al. 1980). In New Brunswick, Tarn (Tarn and Tai 1977, 1983) has, via mass selection within a Group Andigena population, obtained locally adapted clones which in

crosses with Group Tuberosum parents produced heterosis for yield and other traits. In North Carolina, Haynes (1980) conducted both mass and pedigree selection in populations of cultivated diploids based on Groups Phureja and Stenotomum and reported progress in response to selection for long photoperiod, tuber dormancy, tuber dry matter, heat tolerance and resistance to *Alternaria solani*. Carroll (1982) performed mass selection among similar diploid populations in Scotland.

3. Hybridization. In the 1960s Rowe (see Hanneman 1979) initiated selection for adaptation within several populations of wild and cultivated species in Wisconsin. Hanneman (1979) concluded that selection for tuberization within populations of wild species appears to be a very long-term process and that adaptation of wild species can be pursued most efficiently by using Group Tuberosum haploids to hybridize with the wild species initially. Jacobsen and Jansky (1989) have confirmed that it is seldom beneficial to select wild species for tuberization before crossing to selected Group Tuberosum haploids. Hybridization between wild species and Group Tuberosum haploids has resulted in considerable heterosis (Hermundstad and Peloquin 1985).

4. Wide crosses. Several wild species which possess potentially very useful traits are very difficult to cross with *S. tuberosum*. This is the case with the wild Mexican diploid species *S. bulbocastanum* Dun., known for its high resistance to *Phytophthora infestans*. Dionne (1963) discovered that *S. acaule* could be used as a bridging species between *S. bulbocastanum* and *S. tuberosum*. Hermesen (1983) has reviewed the recent utilization of wide crosses in potato breeding. Ehlenfeldt and Hanneman (1984) successfully used a combination of *S. chacoense* as a bridging species, and EBN and ploidy manipulations to transfer *S. brevidens* Phil. germplasm to Group Tuberosum. Helgeson (1989a) has successfully obtained somatic hybrids between *S. brevidens* and Group Tuberosum.

D. Strategies for Germplasm Utilization

The utilization of germplasm in the early years of potato breeding, up to the early 20th century, has been reviewed by Glendinning (1983). The aftermath of the late blight epidemics resulted in a search for resistance to late blight (Howard 1960, 1970; Ross 1986). As a result of the extensive use of *S. demissum* by backcrossing *S. tuberosum* cultivars as males to *S. demissum* × *S. tuberosum* hybrids, a large number of current cultivars are in *S. demissum* cytoplasm (Hermesen 1989). *S. demissum* has probably also contributed to a yield increase in the cultivars derived from it

(Toxopeus 1952). Most cultivars in Europe (Stegemann and Schnick 1985; Ross 1986; Hermesen 1989) and North America (De Jong and Tarn 1984; Plaisted and Hoopes 1989) have various germplasm sources in their pedigree.

1. Backcross. The backcross approach is suitable only if a specific trait needs to be transferred from the germplasm donor to a cultivar. This strategy has been used in attempts to transfer late blight resistance to cultivars (Plaisted and Hoopes 1989). Another example of the use of the backcross method is the transfer of resistance to potato cyst nematodes from wild or primitive cultivated species to cultivars (Ross 1986).

2. Analytic breeding. This strategy was first proposed by Chase (1963) and is particularly suitable for utilizing diploid germplasm in order to broaden the genetic base of tetraploid cultivars. It is essentially a three-phase process: (1) reduction of a polyploid to its diploid components, (2) intensive breeding and selection at the diploid level, and (3) resynthesis and testing of the polyploid form. This method is currently applied in several breeding programs. The initial approach was to develop diploid hybrids by intercrossing *S. tuberosum* haploids with cultivated diploids from Groups Phureja and Stenotomum. Such diploid hybrids tend to be very vigorous. This cultivated diploid germplasm can be used, via sexual polyploidization (Section II. B. 6), to develop tetraploid breeding stocks which exhibit heterosis for yield and other traits. More recently this method has been used to incorporate germplasm from wild *Solanum* species into advanced breeding stocks, again with the tetraploid progenies demonstrating considerable heterosis (Hermundstad and Peloquin 1987; Hermesen et al. 1987; Peloquin et al. 1989). The North American cultivars 'Yukon Gold' (Johnston and Rowberry 1981) and 'Krantz' (Lauer et al. 1988) have been developed by using ploidy manipulations similar to some of those described by Chase (1963). Several advanced tetraploid breeding clones developed by the International Potato Center using ploidy manipulations have been released as cultivars by various developing countries (CIP 1984).

3. Progeny analysis. This is eventually a component of virtually all strategies for germplasm utilization. Progeny analysis can serve as an aid in the choice of parents from both cultivar and germplasm sources and is especially useful in the utilization of adapted germplasm for the development of cultivars and highly adapted parental clones. It has already led to the selection of the first North American cultivar ('Rosa') from hybrid progeny of Groups Tuberosum and Andigena (Plaisted et al. 1981). In an analysis of F_1 hybrid progenies between Groups Tuberosum and

Andigena potatoes, Tarn and Tai (1977) found that the observed heterosis for total yield resulted primarily from the multiplicative interaction of the two yield components tuber number and mean tuber weight. Carroll and De, Maine (1989) reached similar conclusions in a progeny analysis of (tetraploid) Group Tuberosum $\times$ (diploid) Group Phureja clones. A multivariate analysis of parents and progeny can facilitate the identification of superior hybrid families and superior parents (Tarn and Tai 1983). The performance of tetraploid progeny in tetraploid $\times$ diploid crosses cannot be predicted from the phenotypic performance of the parents. Progeny analysis is therefore very important in these ploidy manipulations (Ortiz et al. 1988).

Reciprocal differences in yield and other traits have been reported in progenies between Group Tuberosum and primitive cultivars on both the tetraploid (Hoopes et al. 1980) and diploid (Sanford and Hanneman 1982; Hilali et al. 1988) levels. In these cases the highest yielding progenies were observed when Group Tuberosum was used as the female parent. Although the cause of these differences is still not clear, it may be related to a difference in response to photoperiod (Sanford and Hanneman 1979). It has been suggested that the differences are caused by a chromosomally encoded gene, resulting from maternal and/or paternal effects, rather than cytoplasmic factors (Amoah et al. 1988). If progenies are intended for use as parents then attention must also be paid to potential cytoplasmic male sterilities (Section II. B. 3).

4. Column breeding. Hermesen (1974) proposed the development of "resistance columns" of specific pest resistances. This method is based on the assumption that resistance to a specific pest in different species is based on different genes. After developing highly resistant adapted clones ("resistance columns") within each species, they could then be intercrossed to combine the resistance genes from each species in a breeding line or cultivar.

5. Genetic studies. There is relatively little information available on the genetics of the potato. Various germplasm sources are now being used to conduct basic research on the nature and inheritance of useful traits (Hermesen 1989). The disomic inheritance pattern of the diploids makes this germplasm especially suitable for genetic analysis (De Jong and Rowe 1972). Diploids which produce $2n$ gametes are particularly useful since they can be used for gene-centromere mapping in $4x-2x$ crosses (Mendiburu and Peloquin 1979; Douches and Quiros 1987; Tai 1989).

Trisomics are another useful tool in mapping the potato genome (Wagenvoort and Ramanna 1979; Wagenvoort 1988). The application of isozyme marker and RFLP analysis to diploid germplasm offers a unique

opportunity for the rapid development of a more extensive genetic map in this crop (Bonierbale et al. 1988; Gebhardt et al. 1989; Jongedijk et al. 1990).

6. In vitro gene transfer/genetic manipulation. Several techniques have been proposed for the transfer of genes in potato via genetic manipulation (Ooms et al. 1987; Helgeson 1989a; Masson et al. 1989; Wenzler et al. 1989). Although successful gene transfer has been reported (Boyes et al. 1988; De Block 1988; Tavazza et al. 1988), there may be some problem with low levels of expression of new genes in transformed plants (Yang et al. 1989). Successful expression of transgenic genes in commercial potato cultivars has been reported (Hoekema et al. 1989; Lawson et al. 1989; McPherson et al. 1989), and the results of definitive field trial testing of this material with specific diseases and stresses will be interesting.

7. Induced mutation in vitro. One of the problems associated with inducing mutations in vitro has been the presence in regenerants of gross genetic changes due to chromosomal instability (Karp et al. 1982). Hoekema et al. (1989) have reported that acceptable numbers (97%) of plants with normal phenotypes can be regenerated.

8. Somaclonal variation. Somaclonal variation in angiosperms as a result of in vitro culture has been ubiquitous (Snowcroft 1984). The production of novel sources of variation in potato through somaclonal variation has been reported by Secor and Shepard (1981), Thomas et al. (1982), and Sree Ramulu et al. (1986). Considerable evidence indicates that somaclonal variation may have potential for valuable variation (Weller et al. 1987). Karp et al. (1982) reported that genotype affects the kind of variation observed in potato. Not all tissue culture regeneration systems exhibit somaclonal variation, and this may be due to the low levels of growth regulators used in some tissue culture systems or the short time in culture (De Block 1988).

9. Mutagenic treatments in vitro. Both chemical mutagens and radiation treatments have been used on tissue cultures of potato (Ancora and Sonnino 1987; Sonnino et al. 1987). The mutation frequency increased with increasing dose (Van Harten et al. 1981). Furthermore, a high frequency of mutations was recovered from non-irradiated leaf-discs (12.3%) and petioles (50.3%) (Van Harten et al. 1981). The position of axillary buds on the stem of tissue culture plantlets, and the type of shoot (apical or axillary), affected the mutation frequency of 'Désirée' potato plantlets in vitro (Sonnino et al. 1986).

10. Induced mutation in vivo. Some years ago, there was considerable interest in induced mutations (Luckett 1961). Considerable effort has been expended on recovering mutations from potato clones (Broertjes and Van Harten 1978). However, mutation breeding in potato has yielded few commercial cultivars (Broertjes and Van Harten 1978; Van Harten and Broertjes 1989).

III. CULTIVAR DEVELOPMENT

The cultivated potato, *S. tuberosum*, is an autotetraploid, asexually propagated crop. These two features make the breeding work of the potato quite different from that of a majority of crop plants which are sexually propagated diploid or allopolyploid species. Tetra-allelic genic interactions may result in a high degree of heterosis for economic traits which can be instantly fixed through clonal propagation. Asexual propagation also removes the complexity of evaluating the true merit of progenies due to genetic segregation in the first five or six generations following hybridization between parents. In contrast to these advantages, the breeding objectives for cultivar development are influenced by two major factors: sterility and incompatibility. Unlike small grains which can be increased rapidly through seed, the tuber increase of potatoes typically averages a factor of 10 each generation. Supply and storage of such "seed" tubers of breeding stocks thus constitutes a major constraint in breeding programs. Alternative in vitro propagation methods are discussed in section VIII C.

A survey of potato breeding and genetics programs in Canada and the USA indicated a total of 22 breeding programs growing seedlings for cultivar selection (Pavek 1987). Extensive breeding activities for new cultivars can also be found in Europe, South America, and Asia. The major steps of breeding are similar among most of the breeding programs.

A. The Breeding Plan

A breeding plan represents a logical sequence of activities which in all conventional potato breeding programs contain four common steps: choosing parents and crosses, selection in seedling and early clonal generations, selection in late clonal generations, and evaluation of advanced breeding lines. Table 8.3 provides a brief description of the steps in the Agriculture Canada Potato Breeding Program at Fredericton, New Brunswick.

An investigation of breeding plans of other programs reveals the same major steps, but diversified approaches of selection strategies at

Table 8.3. Steps in the Agriculture Canada Potato Breeding Program at Fredericton, N.B.

Year	Selection Stage and Activity
	<i>Generating the Seedling Population</i>
1	Parents are selected and hybridized to combine traits according to breeding objectives. True seed is harvested.
2	True seed is grown in greenhouses and a single tuber harvested from each seedling. About 120 crosses produce 85,000 tubers.
	<i>Early Generation Selection</i>
3	The 85,000 tubers are grown as single hills. Selection is visual, and is against undesirable plant types, excessively late maturity, and unacceptable tuber types. About 10% are selected for further evaluation.
4	Each of about 8500 selections from year 3 is planted in a 4-hill plot. Selection continues against undesirable traits. About 12% are selected for further evaluation.
5	Each of about 1000 selections from year 4 is planted in a 20-hill plot. The emphasis of selection changes to be positive for desirable yield and tuber traits. About 20% are selected for further evaluation.
	<i>Late Generation Selection</i>
6	Each of about 200 selections from year 5 is planted in a 100-hill seed plot and a 50-hill evaluation plot. Seed multiplication is separate from evaluation from this time. From the evaluation plot, yield is graded and evaluation for quality and disease resistance begins. About 50% are selected for further evaluation.
7	About 100 selections are again planted in 100-hill plots, and evaluation continues as in year 6. About 25% are selected to continue evaluation.
	<i>Advanced Generation Selection in Regional Trials</i>
8	Selections are entered in Advanced Adaptation Trials in the provinces of New Brunswick, Nova Scotia, and Prince Edward Island. Disease evaluation increases, quality evaluation continues.
9, 10, 11	Replicated Regional Trials are conducted in the three provinces (30-hill single-row plots $\times$ 4 reps). As necessary, trials are divided into early and maincrop maturity groups, each with appropriate control cultivars. Disease and quality evaluations continue. The best selections continue in the replicated trials for three years. Only one or two selections per year continue past this stage. In year 11, survivors are sent for virus-freeing and entry into the Canadian seed certification system in anticipation of registration.
12	Multi-row Block Trials compare a single selection with an appropriate control cultivar. Some simple management modifications (e.g., spacing, harvest date) may be tested.
	<i>Commercial Evaluation</i>
13, 14	Commercial Grower Trials provide evaluation of bulk handling and consumer acceptance as fresh or processed (chip or french fry) product.
	<i>Registration</i>
15	A recommendation is made to the Variety Registration Office for registration. The plant description and performance data are prepared for publication. Virus tested seed is available commercially from provincial Elite seed farms.

different stages in the breeding scheme. The breeding schemes used in Europe (Howard 1963; Ross 1986), for example, start selection in the F_1 seedling generation in the glasshouse in year 2 instead of in the seedlings in the first clonal generation in year 3 as in the Agriculture Canada scheme. The progress and percentage of selection over the clonal generations also differ from the Agriculture Canada example. Many factors may contribute to the differences in breeding strategies, examples being choice of breeding objectives, cost of operation, limitation in management practices, and official policy on trial systems. What lies in the center of all the considerations is, however, the efficiency of breeding.

The population breeding scheme adopted by the International Potato Center (Mendoza 1983) aims to produce breeding populations from which national programs in developing countries can select cultivars adapted to their specific growing conditions. The breeding plan emphasizes the creation of populations for stress tolerance and disease resistance more than selection for superior individual clones.

The central series of boxes shown in Figure 8.1 gives a schematic representation of the major breeding steps. A series of boxes describing actions and decision-making processes required during each of these steps is shown to the left-hand side of the breeding steps. Another series of boxes,

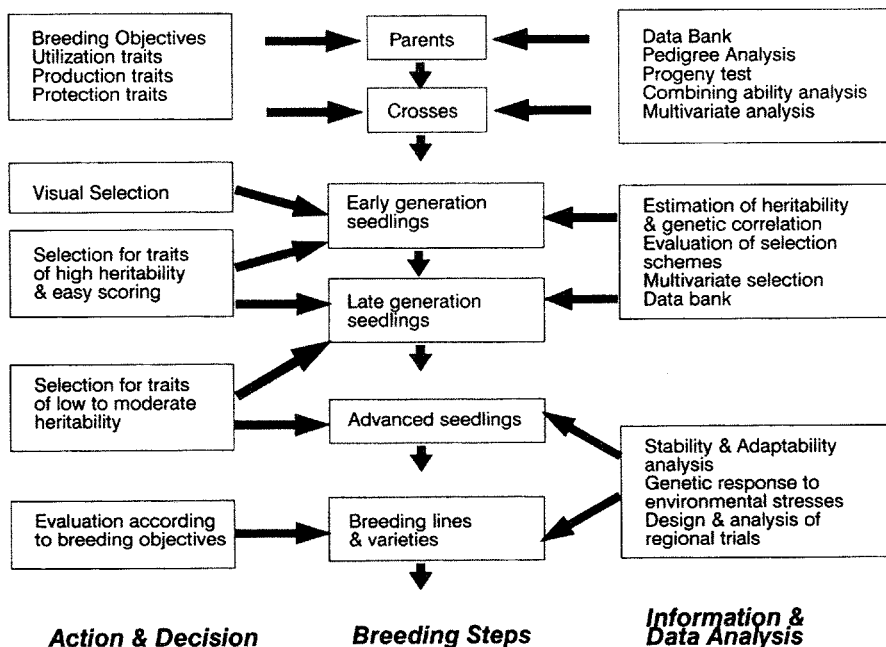


Figure 8.1. Schematic representation of the major breeding steps, their relationship to actions and decision-making processes, and the requirement for information and data analysis.

shown at the righthand side, describes the types of information and data analysis to be employed for assessing and/or supporting the various activities taking place during the breeding procedure. Problems and research progress related to breeding efficiency will be discussed according to the framework set in Figure 8.1.

B. Choosing Parents and Crosses

Parents and crossing combinations between parents should be chosen in accordance with major breeding objectives. It is not realistic to breed for a wide spectrum of utilization objectives. A breeding project designed to meet a special demand in the market, e.g., a cultivar that will french fry, enables a breeder to focus effort on a relatively smaller group of traits and thus allow a greater chance to succeed when compared to breeding for a general purpose cultivar. Also, production and protection traits should be carefully weighed for their importance in terms of adaptation to environmental conditions, response to management practices, and requirements for disease and pest resistances in the growing area.

The sole purpose in establishing a crossing plan is to create a breeding population with high means and wide genetic variability for the traits included in the breeding objectives (Simmonds 1979). A majority of these traits are polygenically inherited. Thus, the first factor to be considered is the relative importance of general combining ability (GCA) and specific combining ability (SCA) in the inheritance of a quantitative trait. Good crosses can be determined based on the GCA information of parents when the GCA of a trait predominates its inheritance. Good crosses can only be chosen by conducting progeny testing experiments on random samples of progenies of crosses available in the breeding program when the influence of GCA is negligible when compared to that of SCA. One way to determine the importance of GCA is to measure the correlation between progeny mean and mid-parent value of many crosses as reported by Maris (1969, 1989). High correlations for traits such as maturity, number of tubers per plant, tuber yield, and under water weight were found in his experiments of hybrid families of Group Tuberosum parents (Maris 1969) and of Tuberosum and Andigena parents (Maris 1989). Inconsistent or low correlations were found for mean tuber weight, date of emergence, and plant height. Plaisted and Cubillos (1972) suggested that the average size of tubers of the progenies can be increased by selecting for large size of tubers in at least one of the parents. Brown and Caligari (1989) found the phenotypic correlations at two sites between mid-parent values and observed values of 10 crosses ranged from low to moderate for breeders' preference, total tuber weight, mean tuber weight, and number of tubers. They cautioned that parental predictions, even when made at limited sites, would be useful if only to eliminate the worst parents.

For the autotetraploid potato, the GCA of a quantitative trait is not only composed of additive genic effects but a portion of genic interactions both within and between loci of the parental genotypes. Further, parental information is not useful for traits heavily influenced by SCA. Thus, it is more secure and reliable to obtain GCA and SCA information for parents and crosses based on progeny test experiments than the parental performance per se. There are many reports on combining ability analysis in the literature. To measure the relative importance of GCA and SCA for various quantitative traits, results of analysis of variance or estimates of variance components in these reports have been used to calculate the variance components of GCA and SCA, and their ratio. Table 8.4 summarizes some of the results based on experiments using Group Tuberosum cultivars and breeding lines as parents. There are extensive reports on combining ability analysis based on genetical materials involving germplasm from other diploid and tetraploid species. Space prevents their review here.

Reports in Table 8.4 indicate that the range of ratios of GCA/SCA variance components for yield is from 0.13 to 2.43. Two of the eight reported ratios show that GCA is clearly larger than SCA, whereas the reverse is true in four cases. The remaining two ratios give equal importance to GCA and SCA. Thus, SCA plays an important role in the inheritance of yield of Tuberosum crosses. Superior crosses for yield should not be dependent on GCA information alone.

The three GCA/SCA ratios for mean tuber weight in Table 8.4 indicate that GCA is slightly or much larger than SCA. Only one in four reports show large SCA effects on tuber number. GCA appears to be important for such traits as maturity, specific gravity, tuber appearance, hollow heart, and tuber protein as results for these traits in Table 8.4 indicate that $GCA \geq SCA$.

There have been few studies on combining ability analysis of quality and processing traits. Killick (1977) reported predominance of SCA for texture and after-cooking darkening, whereas Dalianis et al. (1966) gave a GCA/SCA ratio of 1.51 for the latter trait (Table 8.4). Loisel (1989) reported the GCA/SCA ratios of the color score of potato chips at harvest, after three months cold storage in 6–7°C, and after reconditioning at 22–23°C following cold storage as 2.02, 3.74, and 1.85 respectively. Reports on combining ability analysis of resistances to diseases and pests are equally scarce. Killick and Malcolmson (1973), working with materials of diverse origin, found SCA was important for resistance to late blight. Tai and Hodgson (1975) and Malcolmson and Killick (1980), using exclusively Tuberosum, and Tuberosum and Andigena genotypes respectively, found resistance to late blight was mainly due to GCA effects of the parents. Phillips et al. (1979), working with progenies of parents involving *S. vernei* Bitt. et Wittm., showed that GCA and SCA for

Table 8.4. Estimates of GCA and SCA variance components and their ratio for various quantitative traits based on progeny test experiments of Tuberosum parents.

Authors and Traits	GCA	SCA	GCA/SCA
Sanford (1960, Tables 16, 20 & 23) ¹			
Yield	.705	1.402	.50
Specific gravity	5.093	2.858	1.78
Tuber appearance	.127	.127	1.00
Plaisted et al. (1962, Table 4) ¹			
Yield	.71	3.22	.22
Mullin & Lauer (1966, Table 4) ¹			
Yield	.288	.204	1.41
Tuber appearance	.048	.006	8.00
Dalianis et al. (1966, Table 6) ²			
After cooking darkening	.186	.071	1.51
Tai (1976, Table II) ²			
Total yield	2.06	7.95	.26
Marketable yield	2.44	5.32	.46
Tuber number	98.19	358.81	.25
No. mark. tubers	30.38	87.72	.35
Av. tuber wt.	1310.75	137.56	9.53
Av. wt. mark. tuber	1660.53	248.15	6.69
Specific gravity	10.12	5.60	1.81
Killick (1977, Table 2) ²			
Yield	.064	.500	.13
Mean tuber wt.	360.17	167.60	2.15
% cracked tubers	.801	4.443	.18
Texture	.0058	.0102	.57
After cooking blackening	.0130	.0331	.39
Maturity	.0549	.0038	14.46
Dorozhkin et al. (1979, Table 2) ¹			
Yield	.0017	.0007	2.43
Tuber number	.731	0	—
Veilleux & Lauer (1981, Tables 5, 6, & 7) ¹			
Total yield	.052	.026	2.00
Tuber number	4.39	1.06	4.14
Marketable yield	.032	.030	1.07
No. mark. tubers	1.25	.33	3.79
Hollow heart	.22	.21	1.05
Veilleux et al. (1981, Table 3) ¹			
Tuber protein	.051	0	—
Gaur et al. (1983, Table 1) ¹			
Yield	.070	.063	1.11
Av. tuber wt.	4.73	4.09	1.16
Tuber number	1.15	.04	28.75
Dry matter	.042	.040	1.05
Loiselle (1989, Table 10) ²			
Color score of chips			
—at harvest	.105	.052	2.02
—3 months storage at 6–7°C	.099	.026	3.74
—reconditioning at 22–24°C	.095	.050	1.85

¹Mating design:test crosses; ²Mating design:diallel crosses.

resistance to the white potato cyst nematode were of similar importance.

A survey of results in Table 8.4 indicates the prevalence of GCA effects among quantitative traits. Therefore, GCA information for parents should serve as a useful guide in choosing parents for potentially useful crosses; however, this does not imply that the importance of SCA, and hence the need of conducting progeny test experiments, should be neglected as it does have a significant effect on many traits, especially the important trait of yield.

During field selection, visual discrimination of different progenies in a breeding population was shown to be based on the breeder's visual judgement of a combination of traits (Tai and Young 1984). The proportion of progenies retained in a cross can, therefore, be regarded as a multivariate measure of the merit of the cross. Madry and Ubysz-Borucka (1983) developed a method for combining ability analysis based on the success fraction of progenies in incomplete diallel crosses. They showed the GCA effects of parents were considerably larger than the SCA effects and thus were useful in the prediction of progeny values. Brown and Caligari (1986) examined the usefulness of univariate cross prediction methods and found that predictions based on breeders' preference scores, estimated in any of the early clonal generations, provided a good indication of the potential worth of the cross. Brown et al. (1987b, 1988) reported that the mean preference scores of breeders while judging seedling or first clonal year plants can be used to predict the merit of crosses.

Numerical taxonomic and other multivariate statistical methods have been suggested to increase efficiency in plant breeding (Whitehouse 1969; Sneath 1976). The potato is a multi-trait crop, and this justifies the usefulness of the multivariate approach in measuring not only the combining abilities of parents and crosses in a multi-trait sense, but also the genetic diversity between parents of planned new crosses. Sidhu and Pandita (1980) applied Mahalanobis's D^2 on data of five traits (plant height, stem number per hill, tuber number per plant, average tuber weight, and tuber yield per plant) to classify cultivars. Sidhu et al. (1984) used metroglyph and index score analyses to classify cultivars and breeding lines into groups. Tai et al. (1986) applied cluster analysis on long-term selection records to classify parents into groups and were able to identify superior parental groups. Lynch et al. (1987) used canonical analysis on four quantitative traits (vine maturity, tuber size, marketable yield, and specific gravity) to assess the merit of crosses in relation to established commercial cultivars and breeding goals. Brown and Caligari (1988) investigated three methods of multivariate cross prediction using data of four traits (tuber weight, mean tuber weight, tuber number, and regularity of tuber shape). The best estimates were obtained using multivariate probabilities based on the means, within progeny variances, and

the phenotypic correlation between variates. They also indicated that a sample as small as 25 clones per cross provided good predictions. Tai and De Jong (1980), Tai and Tarn (1980), and Tarn and Tai (1983) used canonical analysis to investigate the relationship between hybrid families and parents for tetraploid-diploid ($4x-2x$) and Tuberosum-Andigena crosses. Schittenhelm (1989) used principal component analysis to compare Tuberosum-Tuberosum and Tuberosum-Andigena crosses.

A critical factor involved in creating a successful crossing plan is the genetic diversity of parents. New crosses obtained from genetically diversified parents help to prevent homozygosity and increase genetic variability of progenies in a breeding population. A severe problem of the current Tuberosum population is its narrow genetic base (Simmonds 1969). Coancestry analysis conducted by Mendoza and Haynes (1974) indicated considerable inbreeding of and kinship relationship between the current cultivars and breeding lines. Table 8.5 gives part of their results on genetic relationships among some of the leading cultivars in the USA. The results of coancestry coefficient of a cultivar to itself (i.e., inbreeding) are equal to or larger than 0.25, which is equivalent to more than one generation of selfing in increased homozygosity. 'Katahdin' contributed to the genetic background of all cultivars (except 'Russet Burbank') listed in Table 8.5. The coancestry coefficient between two cultivars is in many cases equivalent to that of parent-offspring (0.125) or half sibs (0.063). The results suggest the necessity of checking the pedigrees of parents before a crossing plan is carried out so that the potential disadvantage of a narrow genetic base can be minimized. A recent survey by Loiselle et al. (1989a) of inbreeding coefficients for the genotypes of 105 progenies in the Agriculture Canada Potato Breeding

Table 8.5. Genetic relationship among some potato cultivars [Mendoza and Haynes 1974].

Cultivar	Coancestry Coefficient									
	1	2	3	4	5	6	7	8	9	10
1. Cobbler	.250	—	.094	—	—	.031	.043	.057	.078	.098
2. Katahdin		.250	.125	—	.188	.031	.094	.047	.125	.070
3. Pontiac			.250	—	.094	.023	.047	.047	.188	.063
4. Russet Burbank				.250	—	—	—	.094	—	—
5. Sebago					.313	.016	.063	.027	.086	.031
6. Superior						.250	.063	.031	.063	.031
7. Kennebec							.250	.023	.063	.047
8. Norgold Russet								.250	.063	.031
9. La Rouge									.438	.094
10. Norchief										.273

Program at Fredericton indicates a range from 0 to 0.11. No significant relationship was found between the inbreeding coefficients and the proportion of genotypes selected over four clonal generations. Loiselle (1989), however, did find that coancestry coefficients in the 0.10–0.15 range were associated with lower yields.

C. Early Generation Selection

There are three distinct management systems for growing seedlings in early generations. The seedling generation is grown from true seeds, and seedlings are usually planted in small pots in a greenhouse. Clones in the first clonal generation are grown from small whole tubers harvested from the greenhouse-grown seedlings. These clones usually advance to single-hill field plots with the spacing between adjacent plots (60–90 cm) two to three times wider than that normally used in commercial practice. The use of large spacing maintains clear separation of clones during harvesting. As only a small quantity of tubers is available for propagating a clone after the first clonal generation, in the next one to two clonal generations clones are planted in small multi-hill (usually 4–20 hills, see Table 8.3) field plots. This is the first time at which clones can be grown from seed of uniform and normal size, in field plots with “normal” spacing (20–25 cm).

There are two major functions for selection work in the early generations. The population size is drastically reduced so that a small percentage of clones can be carefully evaluated in later generations. The screening method has to be simple and easy to apply as the initial population is very large and any elaborate scoring system would be impractical in terms of cost and time. In most potato breeding programs visual discrimination based on breeder's preference is consequently the choice for screening breeding materials in early generations.

Many studies report poor efficiency of visual selection in early generations (Blomquist and Lauer 1962; Davies and Johnston 1965, 1968, 1974; Anderson and Howard 1980; Tai and Young 1984). Correlation coefficients of visual or breeder's preference scores between seedling and early clonal generations, between early clonal generations grown in separate years and/or sites, and between the same group of clones grown in plots of different sizes (Maris 1966; Tai 1975a; Brown et al. 1984; Brown 1987; Brown, et al. 1987b) were positive but low-to-moderate in magnitude. One factor which may contribute to the poor efficiency of visual selection is the ability of breeders to consistently identify superior genotypes. Brown et al. (1984) found good agreement between breeders in terms of what should, or should not, be selected for seedlings grown in an environment. Tai and Young (1984) reported that compared to discarded clones,

those retained by breeders showed a slightly earlier maturity, reduced plant height, reduced vigor, better tuber appearance, higher marketable yield, and lower total yield. Breeders are thus quite capable of carrying out the task of identifying "commercial type" potatoes by visual selection. As a breeder is influenced by a number of agronomic traits while visually screening seedlings during harvest, low heritability of influential traits may be one of the major causes for the poor efficiency. Correlation analyses of a number of agronomic traits (Zadina 1971; Krug et al. 1974b; Tai 1975a; Brown and Caligari 1986; Caligari et al. 1986; Maris 1988; Neele et al. 1988) indicate low correlations between seedling and early clonal generations and between first and second clonal generations.

Selection of traits of high heritability may improve the efficiency of early generation selection. Selection in the seedling generation is practiced in European but not in North American programs. Several reports have discussed the effectiveness of selecting agronomic traits in the seedling generation. Howard (1963) discarded greenhouse-grown seedlings with long stolons, late maturity, and little vigor. He indicated that selection for low tuber number and tuber shape is not justified. While emphasizing the importance of uniform soil condition and good size (14 cm diameter) pots (Zadina 1971), or standard growing conditions of seedlings in the greenhouse (Krug et al. 1974a, 1974b), low correlations between seedling and clonal generations were observed for several agronomic traits. Świeżyński (1978, 1984) reported that successful selection can be achieved by growing first-year seedlings in the field and selecting plants or tubers based on tuber appearance and size. Low correlations for tuber number and mean tuber weight scored as seedlings in the greenhouse and as first year clones in the field were observed by Brown and Caligari (1986) and Maris (1988). They both reported stronger but moderate correlations for tuber yield. Brown and Caligari (1986) suggested these correlations may have been overestimated because of the association between the weight of the tuber planted in the first clonal year and the resulting yield.

Standard unit heritability (Frey and Horner 1957) of several agronomic traits based on several studies (Tai and Young 1984; Caligari et al. 1986; Maris 1988; Neele et al. 1988) are estimated by simple correlation coefficient between first and second generation clones tested in 1-hill and multi-hill (2–10 hill) field plots (Table 8.6). Heritability of maturity was fairly high, and plant height was moderate. Yield, yield components, and tuber appearance or overall impression in general showed low to moderate heritabilities with the exception of tuber yield reported by Maris (1988). Lynch et al. (1983) tested a random and a selected group of clones in Alberta obtained from the first generation clones grown at the breeding station in New Brunswick, Canada, to determine whether or not preselect-

Table 8.6. Standard unit heritabilities for seven agronomic traits estimated by simple correlation coefficient between first and second generation clones grown in 1-hill and multi-hill field plots, respectively.

Trait	Standard Unit Heritability (h^2)			
	Tai and Young (1984)	Caligari et al. (1986)	Marris (1988)	Neele et al. (1988)
Maturity	.67	—	.78	—
Plant height	.52	—	.47	—
Tuber appearance and general impression	.34	—	.33	—
Marketable yield	.39	—	—	.29
Total yield	.38	.24	.63	.37
Total tuber no.	.31	-.04	.15	.23
Mean tuber weight	.42	.48	.37	—

tion of seedlings from a breeding population grown in eastern Canada would have any negative effect for material distributed for further selection in western Canada. They found that preselection in the first clonal generation at the breeding station in New Brunswick showed limited but significant improvement for maturity, yield, and tuber traits of selected seedlings grown in Alberta, yet did not cause a major reduction in the variability of the traits. The preselection was conducted to eliminate clones with negative traits. All the above results imply positive but low response to selection for agronomic traits, with the probable exception of maturity, when seedlings are grown as 1-hill plots in the first clonal generation.

Neele et al. (1988), comparing simulated selection percentages of about 5%, 20% and 50% in first year clones, concluded that selection efficiency can be optimized only by lowering selection pressure. Tai (1974) and Tai and Young (1984) compared alternative strategies for selecting early generation clones based on selection theory in quantitative genetics and concluded that only a moderate intensity of mass selection over several generations appears to achieve a balance between genetic advance and loss of valuable genotypes.

Visual discrimination is probably the most efficient and economical method for screening seedlings for a number of agronomic traits in a large breeding population in the early generations. Several authors (Tai and Young 1984; Maris 1988; Neele et al. 1988) recommended the use of mild intensity negative selection for seedlings grown in multi-hill plots in the early clonal generations. Negative selection involves the discarding of seedlings with obvious defects, and the retention of those seedlings with no obvious, serious defects. Testing seedlings in multi-hill plots over

several years increases the reliability of early generation selection. Negative (visual) selection with mild intensity reduces the risk of losing valuable genotypes in the breeding population.

D. Late Generation Selection

Late generation selection starts at the sixth year in the Canadian program (Table 8.3). At this stage the number of seedlings are reduced to less than 1% of the original population (Howard 1982; Ross 1986) and are given permanent numbers according to a special coding system. The seedlings are tested in large multi-hill (50 hills or more) plots without replication. The advantage of using large field plots is that the advanced seedlings can be evaluated according to a management system close to commercial practice. The size of the population and the logistics of field operation make a replicated trial difficult to practice. The unreplicated trial, however, can be augmented by a group of cultivars which serve as controls and are replicated according to a special field plot design. This is the augmented design developed by Federer (1956) for testing a large number of breeding lines. Lin and Pouschinsky (1983) developed a modified design for the same purpose which has been adopted by Lynch et al. (1983) for evaluating potato seedlings.

The goal of late generation selection is to identify and evaluate characteristics of superior individual seedlings according to the breeding objectives. This represents a shift of emphasis in breeding activity compared to that in early generations in which group (parent and cross) merits play a significant role in decision making. As every advanced clone is a potential cultivar, a large number of traits, often more than 50, are scored for each clone. The traits include those which are important for utilization, production, and protection in a growing area. Two issues clearly emerge for selection in late generations in addition to those related to the complexity of the field operation: data handling and evaluation.

The best method for handling the large volume of data generated by the late generation clones is to establish a computerized data bank. Young et al. (1980) described an information and retrieval system for use in the Canadian program. Figure 8.2 presents an example of the printout of a clone in this program. It includes information on cross purpose, years of testing, records of traits related to utilization (e.g., maturity, tuber traits, yield, quality traits), production (e.g., top vigor, stolons, digging), and protection (various disease scores), as well as decision information in terms of promotion or demotion of a clone. The data bank is supported by several peripheral programs able to search for superior clones according to special breeding objectives.

As multi-trait data are often available for the advanced clones, it is

PARENTS: E-KING X F58050
PARENTAGE: F34011 K113-1

CROSS: 4901- 4

THEORETICAL

YEAR	CROP	PURPOSE	MULT	STAND	MAT	TOP	B ₀	COL	STOL	DIGS	SK	BR	HH	TYPE	SIZE	AP	TYPE	COL	DEPTH	NO.	EMG	ELV
					1-5	1-5	1-2	1-3	1-3	1-3	1-5	1-5	1-5	1-4	1-3	1-4	1-2	1-3	1-3	1-3	1-4	1-9
1979	M	FF	Y	45	3.0	3.7	2	2.0	2.2	2.0	2.0	2.5	2	4	2.2	2.4	1	1	1.9	2.0	2	5
1980	M	FF	Y	45	3.7	3.6	2	2.0	2.0	2.0	2.0	2.5	1	4	2.1	2.6	1	1	1.6	1.8	3	2
1987	M	EVALUATION	N	95	3.5	3.5	2	2.0	2.0	2.0	2.0	2.0	1	3	2.1	2.6	1	1	1.9	2.0	2	4
1988	M	FF CHECK	Y	95	3.5	3.5	2	2.0	2.0	2.0	2.5	3.0	1	4	2.2	2.2	1	1	2.0	2.0	2	4
AVE.					3.4	3.6		2.0	2.0	2.0	2.1	2.5	1		2.1	2.4			1.8	1.9	2	4

FRENCH FRY

YEAR	S.G.	L	M	S	C	L+M	TEX	COL	FLA	SLC	DIS	TOY	TEX	COL	FLA	DIS	TOY	XAP	XQL	ITX	TX	TOT
							40	30	20	10	10	100	45	30	25	10	100	20	10	20	20	30
1979	1.077	60	15	2	10	121	170	100	115	129	35	22	20	9	0	86	40	24	25	0	89	13
1980	1.084	26	6	1	2	128	146	82	56	131	31	21	20	8	0	80	37	20	25	0	82	14
1987	1.092	33	14	2	3	72	142	114	55	85	34	21	20	7	0	82	41	22	25	0	88	13
1988	1.089	252	150	38	55	81	127	150	94	94	30	17	20	5	0	76	36	14	25	0	75	13
AVE.	1.085					101	146	112	81	110	33	20	20	8	0	81	39	20	25	0	84	13

DISEASE SCORES (1-9)

CHIPPING SCORE											DISEASE SCORES (1-9)														R																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																												
YEAR	FLD		WIA		WIN		40		1		2		3		4		LANG		SCAB	BLIGHT		B		V		L		E		S		C		O		L		R		A		P		I		M		Z		OTHER																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																			
	DIR	55	55E	55L	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK		WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	WK	

YEAR	OUTSIDE TRIALS	COMMENTS	DIS	T-HILL	RETAIN	BENTON
						P-TON

1979 CT SEED PLOT
1980
1987
1988
LENGTH, SIZE, DID NOT GO TO PIECES. IT HAS ENOUGH EYES.
LONG, A LITTLE THIN, NOT PRETTY BUT OK. POINTING BOTH ENDS. SHRIVELING.
AN AVERAGE SHEFFY RUN
POOR SKIN, LIGHT RUSSSET, VERY IRREG TUBER TYPE, HEAVY SET, PCR RUN.

Figure 8.2. Computer print out of information on a late generation selection in the Agriculture Canada Potato Breeding Program at the Fredericton Research Station.

F69016 10

advantageous to apply multivariate selection methods to the evaluation process. Information on the use of multivariate methods for the evaluation of clones in a potato breeding program is scarce. The potential is yet to be exploited. Loiselle et al. (1989b) studied the use of several multivariate methods to eliminate redundant variables used for evaluating chipping quality of late generation clones in the Canadian program. This analytic study showed that the number of traits required for evaluating good chipping clones can be reduced to four from the original eight without losing much of the efficiency of evaluation. This helps reduce the cost of data collection while maintaining selection efficiency.

E. Evaluation of Advanced Selections

There are two phases for evaluating advanced selections. Clones selected from the late clonal generation are screened in a series of preliminary trials which are carried out over several seasons and/or sites in the growing area. Cultivars and breeding lines introduced from other programs may be included in the trials. The emphasis here is to identify superior genotypes based on an evaluation procedure which minimizes the disturbances due to genotype $\times$ environment (GE) interactions within an acceptable cost of operation. The information which is useful for determining the appropriate type and size of trials for the preliminary screening of advanced clones is data obtained from a group of representative breeding lines and cultivars tested over a series of experiments over years and locations. Analysis of variance followed by estimation of variance components enables the breeder to measure broad-sense heritability and genetic advance to selection of quantitative traits under different combinations of experimental conditions such as replications per trial and numbers of years and locations used for evaluation. Plaisted (1957) gave a good example of the variance component analysis of specific gravity. Sekioka and Lauer (1970) analyzed five traits based on trials conducted for three years over four sites. Their data, however, were obtained from only five cultivars. Many studies on estimation of genetic parameters (Torres et al. 1974; Gaur et al. 1978a, 1978b; Pandita and Sidhu 1981; Murakami 1983; Birhman and Kaul 1989b) are based on data of a single experiment. Their results may grossly overestimate the genetic parameters such as the broad-sense heritability and genetic advance when GE interactions are important in the expression of quantitative traits.

Superior clones selected from the preliminary trials are evaluated in a series of regional trials. The trials are replicated and conducted over several years and locations. The purpose of the trials is to evaluate individual clones and new cultivars not only in terms of the average per-

formance of important traits over the trials, but in their response to the environments. GE interactions are no longer regarded as nuisances that mask the real genetic potential, but as an essential measure of the stability and adaptability of genotypes in response to environmental stresses in a growing region. Various statistical models have been investigated for their usefulness in interpreting GE interactions such that genotype response to environments can be evaluated, compared, grouped, or even predicted. Plaisted and Peterson (1959) estimated the variance component of genotype-location interactions for each of the possible pairs of genotypes which were tested at a number of locations in one year. The average of the estimates for all combinations with a genotype in common was considered as a measure of the adaptability of the common genotype. A linear regression model (MacKenzie et al. 1976), which regresses performance of individual genotypes tested in a series of trials on the site means, was found useful for identifying those genotypes which would perform well for such traits as yield and processing quality over a range of growing conditions. A linear model for genotypic stability analysis of breeding lines and cultivars tested in regional trials was proposed by Tai (1971). Tai and Young (1972) further proposed to use the mean performance and estimates of the two genotypic stability parameters of each of the genotypes tested in the trials to characterize their adaptability as general, specific, or poor.

Multivariate methods have been investigated for their usefulness in grouping genotypes according to their pattern of response to the environments, or in revealing the dynamic interplay between genotypes and environments. The analytic results not only assess the potential of new selections, but provide useful information on environment and management practices. Cordeiro et al. (1983) conducted analyses of stability and genotypic similarity in a set of cultivars. They showed that differences in cultivar behavior were associated with mean yield of cultivars, response to non-identified environmental effects, and regression on an environmental index measured by trial means. Lynch and Kozub (1988) used cluster and principal component analyses, together with joint regression analysis, to study the response of a group of genotypes to a set of diverse prairie environments in western Canada. The results suggested the elimination of some test sites which do not contribute additional information. For marketable yield, both cluster and principal component analyses can be used to group cultivars. A statistical model on path analysis of GE interactions of yield proposed by Tai (1975b) was found useful for interpreting the dynamic interaction between genotypes and environments for the development of yield based on data obtained from a series of trials carried out over several years and sites (Tai 1979), or determining the response of genotypes to water stress (Lynch and Tai 1989).

Tai and Young (1989) suggested the use of a limited number of control cultivars to index environments based on principal component analysis. Stepwise regression analysis of yields of a genotype on the environmental indices was used to construct a performance model for the genotype. The performance model was then proposed as a prediction tool.

One factor critical for the successful comparison of advanced selections is the use of the proper size and shape of trial field plots. Only a few reports are found in this area of research. Mountier (1985) made a survey of several reports and indicated that long narrow plots are better than short wide ones. He recommended the use of a 4-row plot with a length of about 5 m. Pemajayantha and Gunasekara (1982) suggested that either square or oblong plots can be used for potato experiments. Simmonds (1980) compared the yields of four cultivars in trials and in commercial production, and found the two agreed rather poorly. Leon (1987) pointed out that the inaccuracies of small plot yield trial data in the estimation of farm scale yields is caused by competition of cultivars grown in adjacent plots. This can be reduced by increasing the number of rows per plot. Most North American trials for comparing cultivars and breeding lines use long single-row plots. A block trial (Table 8.3), however, is used to evaluate the performance of the most advanced selections at the farm scale. Another issue in comparing cultivars in trials is the use of proper sample size for estimating such tuber traits as specific gravity, cooking, and processing quality. Young and Cannon (1964) investigated field plot technique for the estimation of specific gravity. It appears that no similar studies have been carried out on other tuber traits.

IV. PRODUCTION TRAITS

Production traits include those which respond to environmental factors and various management practices during growth for achieving satisfactory production of a crop. Most of the traits in this category are physiological or morpho-physiological traits which regulate the growth of the potato. Moorby (1982) provides detailed information on the physiology of growth and tuber yield, and a new edition of Burton's book *The Potato* (1989) includes an extensive review of physiology.

A. The Ideotype

Van der Zaag and Burton (1978) recognized three levels of yielding ability in the potato: actual, attainable, and potential. Actual yield represents the current commercial productivity. Attainable yield is that

obtained by applying the best available growing techniques which would be commercially justifiable in a growing area. Potential yield is what could be expected from an ideotype. The potential yield in western Europe is estimated as 100 tons/ha, whereas average actual yields in the highest production area in Europe is 40 tons/ha. Two factors are identified by Van der Zaag and Burton (1978) as critical for achieving high productivity, namely the length of the period of tuber growth and the daily tuber growth. They also point out that the real goal of production is to maximize the usable yield; thus, another factor is tuber setting. A potato ideotype is the one which is capable of producing a high set of tubers and maintaining the longest possible duration of a high rate of tuber growth.

B. Plant Architecture

Potato production in temperate zones is limited by the length of growing season which is roughly from April to October in northern latitudes. To maximize the period of tuber growth the crop must develop a full leaf cover early (Haeder and Beringer 1983), initiate tubers at the beginning of June, and be productive until September (Van der Wal et al. 1978). One trait related to the length of the tuber growing period is the physiological age of seed. Compared to physiologically young seed tubers, old seed tubers emerge earlier and initiate tubers earlier, but have a shorter tuber bulking rate and earlier senescence (Wurr 1982). Another trait which contributes to the length of the period is the ability of the seed tubers to emerge in low soil temperatures after planting (Van der Wal et al. 1978). An extended productivity of the canopy towards the end of the growing season prolongs the period of tuber growth (Haeder and Beringer 1983), but this implies undesirably late maturity of the foliage.

Numerous physiological traits are associated with the rate of tuber growth. A suitable leaf area with a high photosynthetic rate after tuber initiation, a deep and wide spread root system, and an optimum distribution of dry matter between haulms, roots, and tubers are essential factors regulating tuber growth (Van der Wal et al. 1978; Van der Zaag and Burton 1978). A number of plant traits are linked to the efficiency of photosynthesis. These include foliage type (erect vs spreading) and size, leaf:stem ratio, shoot:tuber ratio, leaf number, thickness, area, and the rate of successive leaf appearance during growth, light interception, and respiration (Van der Wal et al. 1978; Van der Zaag and Burton 1978; Scott and Wilcockson 1982; Haeder and Beringer 1983). Iwama and his colleagues (Iwama et al. 1979; Iwama et al. 1981; Iwama and Nishibe 1989) identified a number of root characteristics related to production including morphology, respiration, dry weight, length, and surface area.

Van der Zaag and Burton (1978) pointed out the haulms and roots used about 20% of the total dry matter produced. Dry matter distribution is often measured by the harvest index (Neele 1989; Spitters et al. 1989).

C. Breeding Implications

1. Tuber dormancy and seed age. Physiologically old seed tubers produce plants which emerge faster, initiate tubers earlier, bulk more slowly, and senesce sooner than those from younger seed (Wurr 1982). These traits are apparently only suitable for early cultivars. Potatoes which sprout readily in storage are particularly not desired for use in processing. Breeding for desired duration of tuber dormancy would provide proper control of sprouting behavior. Bogucki and Nelson (1980) found that cultivars were different from each other in the length of dormancy and sprouting characteristics. Genetic and breeding studies of dormancy and sprout growth have focused on diploid potatoes (De,Maine 1978b; Thompson et al. 1980) mainly because diploid species such as *S. phureja* currently used in breeding programs have short dormancies. De,Maine (1978b) reported that GCA was more important than SCA for the rate of sprout growth. High additive genetic variance was also reported by Thompson et al. (1980). Another role that the physiological age of seed plays is in cultivar testing. Scott and Wilcockson (1982) and Wurr (1982) advocate that it is useful to assess new cultivars over a range of physiological ages to demonstrate their performance potential under contrasting cultural conditions.

2. Rate of emergence. Potatoes are usually not planted in the temperate zone until the danger of frost is over. A desired trait is a high rate of emergence even when the soil temperature is low. Cultivars respond differently to storage management in terms of sprouting behavior, but no breeding activity is in progress to screen for emergence ability at low temperatures (Van der Wal et al. 1978).

3. Foliage. An ideal foliage develops full leaf cover early (Haeder and Beringer 1983), maintains an optimum leaf area index of 4–5 (Haeder and Beringer 1983) and an optimum rate of new leaf appearance (Van der Wal et al. 1978), keeps proper leaf position and thickness for best light interception and leaf:stem ratio to avoid lodging (Van der Wal et al. 1978), and is photosynthetically active until fall (Scott and Wilcockson 1982). However, the breeding implications of some of these traits on productivity are not certain (Van der Zaag and Burton 1978). Selection for genotypes able to expand leaves more rapidly in spring may also require

frost hardiness in some regions, and advancing leaf growth in spring seems linked with advanced senescence (Scott and Wilcockson 1982). Świeżyński et al. (1978) demonstrated genetic differences between clones in early growth of shoots and roots and the root:shoot ratio. They found that early shoot growth was associated with early tuber growth and a short growing period, whereas a higher root:shoot ratio delayed tuber formation and was associated with a longer growing period. They did find clones which combined the two characteristics. Neele (1989) found that the early start of foliage growth was dominant over a later start, whereas the relative growth rate of the foliage was additively inherited.

4. Photosynthetic rate and tuber dry matter. Zrust and Smolikova (1977) suggested the use of assimilation rate measured during a period of growth to screen parents. Zrust (1983) used a gravimetric disc method to measure photosynthetic rate in leaves and detected differences between genotypes. Dwelle et al. (1979) found the product of gross photosynthetic rate and leaf area showed a high correlation to final yield, and suggested these two traits can be used as a selection tool for high yield. Spitters et al. (1989) reported the differences found in cumulative light interception between cultivars were mainly due to differences in time of foliage senescence. Late cultivars had a lower harvest index and a higher tuber dry matter content, but there was no relation between lateness and light utilization efficiency. A relatively high heritability was found for cumulative light interception and tuber dry matter content, and thus both can be used in breeding. In fact, specific gravity is a trait showing small genotype-environment interactions (Killick and Simmonds 1974). Neele (1989) found the early onset of tuber growth was dominant over late, and the increase rate of the harvest index was additively inherited.

5. Root system. Van der Zaag and Burton (1978) and Van der Wal et al. (1978) suggested that water deficits during growth reduced daily growth rate of the tubers. They believed this to be the main cause of the gap between actual and potential yield. Improvement of the root system is apparently required for increasing drought resistance and consequently yield. Iwama et al. (1981) compared 280 unselected clones and found those with larger root dry weight, stem dry weight, and leaf dry weight tended to have a longer growing period and higher yield. Iwama and Nishibe (1989) compared morphology, respiration, dry weight, length, and surface area of the roots of a number of cultivars and wild relatives. They found root dry weight is associated with the bulking rate of tubers. The wild species in their study showed a larger root dry weight, length, and surface area, and a higher root:shoot dry weight ratio than the cultivars and breeding lines. This suggests that the former should have good

potential as parents to improve root characteristics. It should be noted, however, that a heavy root mass with high penetrating power, while beneficial for increasing yield, poses problems in mechanical harvesting operations. Some breeding programs, such as the Agriculture Canada program at Fredericton, select against seedlings with heavy and fibrous root systems.

At the present time, it is difficult to identify which physiological traits should be used in a breeding program. As noted by Gmelig Meyling and Bodlaender (1981), the genetic differences in productivity are not caused by one single growth or development parameter. There are very few breeding activities aimed at screening for physiological traits, and further breeding for physiological traits probably depends on research to develop efficient evaluation techniques.

V. UTILIZATION TRAITS

A. Nutritional Traits

The nutritional value of the potato is excellent (Woolfe 1987). It provides relatively few calories for its bulk, the protein is high quality, and it is a good source of water-soluble vitamins including ascorbic acid (vitamin C) and the B vitamins thiamin, pyridoxine, and niacin. It can provide a significant amount of a number of minerals including iron, magnesium, and phosphorus. Only a few of these components have received significant attention from a breeding and genetic perspective.

1. Starch (dry matter content or specific gravity). Potato tuber carbohydrates may be classified as starch, non-starch polysaccharides, and sugars. (Sugars are discussed under "Processing Traits" in section V D.) Starch, at 60–80% of tuber dry matter, is by far the largest component of the solids content (Woolfe 1987), and since the relationship between starch and total solids is relatively stable, dry matter content is usually equated with starch content (Gray and Hughes 1982). Although such relationships do not always hold true because of the influence of environmental and management practices, and other components of quality (Gray and Hughes 1982), for the purpose of comparing selections under similar conditions in a breeding program dry matter is a fairly reliable indicator of quality. Dry matter gains additional importance because it is frequently used as a measure of tuber quality, and is an important trait for processing. Dry matter in turn is usually estimated by specific gravity or sometimes by under-water weight. Procedures for measuring specific gravity have been reviewed by Smith (1987), but new computerized

methods have already been described (Tai et al. 1985). One important but rarely considered aspect of specific gravity estimation, that of sample size, was addressed by Young and Cannon (1964). Discrepancies in the determination of specific gravity and starch content, and the relationship between them, have been critically reviewed by Samotus et al. (1986).

Specific gravity shows small genotype $\times$ environment interactions (Killick and Simmonds 1974). Heritabilities are generally moderate to high in both diploid (Haynes et al. 1989) and tetraploid (Tai 1976; Killick 1977) material, and GCA predominates over SCA (see Table 8.4). Correlations of specific gravity with other traits have been discussed by Killick (1977) and Ross (1986), and there appears to be no constraint to continuing selection for higher values.

Potato starch is composed of amylopectin (highly branched chains) and amylose (relatively unbranched chains) in a ratio of about 3:1 (Talbert et al. 1987); these proportions can be changed by selection (Rothacker and Effmert 1968). Recently an amylose-free mutant has been isolated from *S. tuberosum* (Jacobsen and Feenstra 1989).

2. Proteins. Present potato cultivars average about 2% protein on a fresh weight basis. This protein has a high biological value, and the production per unit area of crop is second only to soybean, but in most developed countries the potato is regarded as a carbohydrate food (Holden 1981). Protein composition of the potato has been reviewed by Woolfe (1987). The 1970s were an active period for the study of potato tuber proteins, and it was established that protein content could be increased through selection; heritabilities were moderate, and protein levels of 18% (on a dry weight basis) could be achieved (Holden 1981). Selection for both high protein and high dry matter and high yields was considered possible (Holden 1981; Ross 1986).

The most prominent tuber protein is patatin, a glycoprotein, that makes up to 40% of the total soluble protein. Variations in patatin have been investigated by Jervis et al. (1986), and Rosahl et al. (1986) have determined that it is encoded by a multigene family and have characterized a patatin gene. Another development is the expression in transformed potato plants (albeit at a low level) of a synthetic gene for improved protein quality (Yang et al. 1989).

3. Vitamin C. Potatoes are an excellent source of vitamin C (ascorbic acid) (Woolfe 1987). The content varies with cultivar, but also with crop management and storage conditions (Salunkhe et al. 1989). Sinden et al. (1978) estimated a narrow sense heritability of 0.45 and concluded that the level of ascorbic acid could be increased through breeding and selec-

tion. However, there seems little interest in pursuing this objective in developed countries at the present time (Holden 1981; Ross 1986).

B. Glycoalkaloids

Glycoalkaloids above threshold levels impart a "bitterburn" taste to potatoes (Zitnak and Filadelfi 1985). In the 160 years since their first isolation (Osman 1983), and especially since the release of 'Lenape' (B5141-6) in the USA and its subsequent withdrawal because of high total glycoalkaloid (TGA) levels (Zitnak and Johnston 1970), these compounds have received much attention. Their chemistry, toxicity, and genetics have been reviewed many times (e.g., Coxon 1984; Sinden et al. 1984; Roddick 1986; Morgan and Coxon 1987). Glycoalkaloids are assured a continuing importance since while low levels are required in the tubers, high levels occur in the foliage of many species and are associated with resistance to diseases and pests (Kuc 1984; Roddick 1986; Van Gelder et al. 1988).

It is widely accepted that 20mg/100g fresh weight of TGA is the acceptable upper limit for cultivars (Holden 1981; Sinden et al. 1984). At this level a bitter taste can be detected (Sinden et al. 1976; Ross et al. 1978; Zitnak and Filadelfi 1985), and it is at the lower end of the 20–38mg/100g range which is preferred by the potato-consuming Aymara Indians of the Bolivian altiplano (Johns and Keen 1986). In practice potato cultivars rarely exceed this critical level (Sinden and Webb 1972; Ross et al. 1978; Davies and Blincow 1984), although levels may rise considerably in damaged tubers (Olsson 1986). TGA levels may also increase under the same light conditions that cause greening (section V E 1), although the biochemical pathways are unrelated. Potato peel usually contains more than half of the glycoalkaloids in the tuber, and these can be removed by peeling (Sinden et al. 1984), but fried potato skin products may have high levels (Osman 1983).

Successful screening is dependent on suitable test methods which have been reviewed by Coxon (1984). These continue to see rapid improvements especially in HPLC methods (Osman and Sinden 1989) and ELISA methods (Morgan et al. 1985; Hellenas 1986).

Heritability estimates for TGA vary (Sinden et al. 1984), but as long as the trait is segregating breeders can select low value clones. Although 'Lenape' was withdrawn from the market it has continued to be successfully used as a parent (Ross 1986). Breeders are cautious about releasing selections that approach the 20mg/100g value, and a 6mg/100g limit may become a more realistic guide (Ross et al. 1978; Parnell et al. 1984). High TGA selections are normally identified and eliminated by taste panels

(Ross 1986), but analytical tests are increasingly required for cultivar release. Formal procedures for these are not always in place (Holden 1981), and though Parnell et al. (1984) have suggested a basis for sampling there is not yet a generally accepted analytic procedure.

C. Fresh Consumption Traits

Many utilization traits are important whatever the end use of the cultivar since apart from such industrial uses as starch at least a part of the crop of most cultivars is sold in the fresh market. These traits are discussed in this section. However, several traits do not fit into such clear categories. The depth and appearance of the skin, in the sense of its smoothness and brightness as separate from russetting, is rarely discussed although it is important for consumer recognition (Gray and Hughes 1982). Appearance in this general sense is mainly determined by GCA (section III B). Uniformity of tuber size, determined in part by the cultivar tuber setting behavior, is also important from a grading and marketing perspective (Gray and Hughes 1982).

1. Tuber dormancy. Tuber dormancy has been discussed in the context of physiological age and plant development in section IV C 1. A different aspect of long dormancy relates to the maintenance of good tuber quality for fresh and processing markets after storage for as long as seven months (Hoopes and Plaisted 1987). This is increasingly important as consumers expect potatoes free from sprout inhibitor residues. There are large differences in dormancy in cultivars (Holden 1981), and a high additive genetic variance has been reported in diploids (De, Maine 1978b; Thompson et al. 1980). Dormancy has also been changed rapidly in a tetraploid Group Andigena population (Tarn 1981). This trait can thus be readily modified by breeding and selection. A method for assessing dormancy is recommended by Reust (1986) but requires a sample of 40 tubers. In view of the high heritability and low reported genotype $\times$ environment interactions (Thompson et al. 1980) selection may be carried out earlier with a smaller sample size.

2. Tuber shape. Shape is determined by a major gene, perhaps in combination with some minor or modifying genes (Maris 1962). In cultivated diploid potatoes this gene is apparently linked with a gene controlling anthocyanin pigment distribution (De Jong and Rowe 1972). Since length is recessive, and the recessive genes may be carried by round parents, the selection of good long crosses is dependent on recognizing superior cross combinations rather than superior parental clones. However, it is not

usual to make crosses of the type "long" with "long" since their progeny often contain a high proportion of long but thin and useless tubers (Howard 1982).

3. Eye depth. In a study of progenies from several cultivars Maris (1962) concluded that the inheritance of eye depth is determined by one major gene with a cumulative effect, and with shallow eyes recessive. He also found evidence that shallow eyes appear to be linked to long tuber shape. Deep eyes in some of the diploid Group Phureja—haploid Group Tuberosum hybrids used in North American programs have been passed to the progeny (De Jong and Tai 1977), but more recent diploid hybrids involving several wild species consistently have shallow eyes (Hermundstad and Peloquin 1986).

4. Russet skin. The inheritance of russet skin type was found by De Jong (1981) to be determined by the complementary action of three independently segregating, dominant genes. This mode of inheritance increases the difficulty in breeding good russets, and since non-russet parents may be carrying some of the genes the selection of good russet crosses is dependent on recognizing superior cross combinations rather than superior parental clones.

5. Skin color. Pigmentation genes divide into three categories: (1) genes controlling the presence or absence of anthocyanin pigment production, (2) genes controlling pigment distribution within the plant, and (3) genes controlling the specific chemical composition of the anthocyanins. The genetics of skin anthocyanin pigmentation in potatoes is well known and has been reviewed by Howard (1970). All of the pigment distribution genes described thus far are linked, including that for the distribution of anthocyanin to the tuber flesh (De Jong 1987). The shade and intensity of the red, blue, or purple coloration is determined by the genotype.

6. Flesh color. Yellow flesh is associated with the presence of carotenoids (Gray and Hughes 1982), and the yellow color is dominant over white and controlled by a major gene with modifying genes for different degrees of yellowness (Howard 1982). The inheritance of anthocyanin pigmentation of tuber flesh has been described by De Jong (1987).

7. Texture and sloughing. Texture is probably the most important sensory trait of cooked potatoes yet is associated with so many component variables, and influenced by so many environmental factors, that the breeder is generally content with a broad overview. Reviews of potato texture by Warren and Woodman (1974) and Gray and Hughes (1982) illus-

trate all these difficulties, and more recent investigators continue to discuss definitions (McComber et al. 1987), instrumental measurement (Böhler et al. 1987), and sensory evaluation (Böhler et al. 1986).

A practical terminology recommended by the European Association for Potato Research (Lugt 1961) for the assessment of cooking quality includes gradations for each of five components of texture, namely disintegration (sloughing), consistency (firmness), mealiness (sometimes called flouriness), moistness, and structure (coarseness). This has been extended to processing potatoes by Keller and Baumgartner (1982) and slightly modified by Ross (1986).

Holden (1981) argues that since potatoes with different culinary and processing uses have different textural requirements that are mutually exclusive, one of the most important aspects of tuber quality is stability of expression of the attribute. While Holden was primarily considering variation over cultivars, sites, and years, this is also important within a cultivar because of the variation in time of tuber set, and in tuber maturity at harvest (see section IV). This in turn leads to the importance of adequate sampling (section V A 1). The uniformity of samples is important since the detection thresholds of taste panels can be as low as 0.004 units of specific gravity equivalent to a mean total solids difference of 1.05 g/100 g (Murphy et al. 1967). Alternatives to sensory panel evaluations, using scales similar to those proposed by Lugt (1961), have been proposed by Davies and Dixon (1976) who found very high correlations between taste (mouthfeel) and visual assessments of texture, and by Chubey and Mazza (1983) who found a significant correlation of the amount of sloughing between conventionally cooked samples and plugs cooked in a pressurized system.

Macarthur and Killick (1976) found cultivar differences for sloughing, texture, and specific gravity, and found that all three were highly correlated. Since specific gravity is the easiest of these traits to score they conclude that selecting for this trait would permit sensible selection for texture and sloughing. Specific gravity is the first evaluation of texture in most breeding programs, and sensory evaluation by taste panels is carried out at later stages of selection. In a further study, Killick (1977) determined that SCA was important in the inheritance of texture and that good parental combinations could only be identified by trial crosses.

8. Flavor. Cooked potato flavors are very complex and vary with both the chemical components and the means of preparation (Ross 1986; Josephson and Lindsay 1987). While flavor is considered difficult to assess (Holden 1981; Howard 1982), the increasing consumer interest in quality may mean breeders should be paying more attention to this trait. It may be time to move away from selecting against off-flavors (Holden

1981), to using organoleptic tests and appropriately organized taste panels to identify selections with more subtle but positive flavors.

9. Enzymic browning. The oxidation of phenolic compounds, primarily the amino acid tyrosine but also chlorogenic acid, by phenolase to produce first a reddish orange then a dark brown coloration is well understood (Gray and Hughes 1982; Salunkhe et al. 1989). This enzymic browning only occurs when tubers are cut or bruised, and cultivar is a major factor in its expression.

It is a trait that is probably increasing in importance with the growth of prepeeled products in institutional and similar markets. It is thus encouraging that Mondy et al. (1985) found that selections resistant to golden nematode had lower phenols and discolored less than tubers from nematode-susceptible clones. A lack of enzymic browning has been found by Gubb et al. (1989) in the Mexican tetraploid, 2EBN species *S. hjertingii* Hawkes.

10. After-cooking darkening. After-cooking darkening, which occurs as a grey, blue, purple, or black discoloration predominantly at the stem end, has been reviewed by Gray and Hughes (1982) and Smith (1987). It is caused by complexes of iron and chlorogenic acid, and also iron and ascorbic acid (Muneta and Kaisaki 1985). Killick (1977) reports significant SCA for this trait, and Howard (1982) reports that it is a highly heritable trait with at least 20% of a progeny resistant if one parent has good resistance. Although Smith (1987) claims that breeding for resistance has produced little success, there is agreement on the importance and practicality of discarding those clones that show discoloration (Holden 1981; Hunnius 1981; Ross 1986; Hoopes and Plaisted 1987). There seems no reason why new cultivars should show little or no after-cooking darkening.

D. Processing Traits

In many developed countries as much as 40% of the potato crop is processed as french fries and chips (crisps). The most important component in determining the processing quality is sugar content since it is closely related to the color of the products (Talburt et al. 1987). There are three major sugars in potatoes: sucrose, fructose, and glucose. Sucrose, the non-reducing 12-carbon sugar, is the dominant sugar which can reach as high as 9 mg/g of tuber during tuber growth (Gould and Plimpton 1985). It is converted to starch during growth and should drop to a low level at harvest. Fructose and glucose are 6-carbon reducing sugars which remain low and at about the same level throughout the harvest period (Nelson

and Sowokinos 1983). Storage of tubers at temperatures below 9–10°C results in a substantial increase in sugar content (Coffin et al. 1987) due to the accumulation of sucrose and the subsequent conversion of sucrose to reducing sugars (Sowokinos 1978). During frying, the aldehyde groups of reducing sugars react with the free amino groups of the amino acids and proteins in a Maillard reaction that causes dark colored products (Talbert et al. 1987). Of the two major processing products, chips suffer more from the problem of high sugar concentration than do french fries because the surface sugars of raw tissue of french fry strips can be leached out with water (Weaver and Timm 1983).

As pointed out by Talbert et al. (1987), the accumulation of sugars in cold storage can be reversed by reconditioning at room temperature (about 2–3 weeks at 16–22°C). Another method of achieving a low sugar level is to store potatoes at 10°C which represents a compromise between excessive sugar formation on the one hand and early sprouting on the other. Only some cultivars, however, respond to these treatments, as evidenced by the release of new cultivars specially designed for chips or french fries. Cultivars differ in their response to chilling through variations in sugar accumulation (Ewing et al. 1981; Coffin et al. 1987). Cultivars which have the inherent ability to reduce their translocated sucrose pool to about 0.25% (2.5 mg sucrose/g tuber), and maintain an equilibrium level of reducing sugars of 0.15% or less in storage, have the potential to produce light-colored chips after long-term storage (Nelson and Sowokinos 1983).

Breeding for cold temperature processing ability is a major goal in contemporary breeding programs for processing potatoes (Johansen 1986; Coffin et al. 1987). Two components are required to be incorporated into a breeding program for cold temperature processors. The first is the source of low sugar parents, and the second is the genetic knowledge of the trait plus an efficient and accurate screening method. Primitive cultivars are a valuable source of cold processing ability. Lauer and Shaw (1970) found genetic materials in *S. phureja* for breeding chipping potatoes from cold storage. Johansen (1986) indicated *S. phureja* and *S. andigena* are both good sources for producing progenies that chip out of relatively cold storage and are good reconditioners. Many of the potential chip selections in the North Dakota, USA, breeding program have *S. phureja* or *S. andigena* in their pedigree.

The genetics of all traits related to processing ability are not clear at present. Ross (1986) indicated that the content of reducing sugars and its responses to cold temperature storage and reconditioning may be under the control of separate mechanisms. Loiselle (1989) studied the inheritance of visual scores of chip color and found two essential components of the chip performance of hybrid progenies tested under different

conditions, namely an "overall chipping ability" component and a "chipping stability" component. Accatino et al. (1973) reported two dominant genes controlling the response to reconditioning, and one of the genes must be present to prevent darkening during processing. Ehlenfeldt et al. (1990) crossed two low reducing sugar clones with two cultivars used by the chipping industry and found the distributions of families were skewed towards the high parents. Low percentages of progenies with low reducing sugars were found in the crosses.

Selection for processing qualities in most breeding programs, like the one used by the Agriculture Canada program at Fredericton, is based on sensory judgement of various attributes such as color, flavor, and texture of the processed products (see Figure 8.2). Direct screening of sugars in the tubers is still in the development stage. Various procedures have been suggested. For example, Sowokinos (1978) and Nelson and Sowokinos (1983) found that sucrose levels measured during early tuber development may be used to screen for chipping quality of seedlings after moderate- to long-term storage. Weaver and Timm (1983) suggested, as a screening tool for processing potential, the use of the fructose:glucose ratio measured from potatoes harvested from 110-day-old plants. This procedure, however, runs a risk of showing a high ratio, which is considered as indicating a low reducing-sugar accumulation, when in fact both components are high. There are also several methods for the determination of sugars in tubers, which can be categorized as chromatographic, colorimetric and instrumental procedures (Mazza 1983; Gould and Plimpton 1985). None of these methods, however, appears to be an efficient and accurate procedure suitable for screening large numbers of seedlings. Otazu and Secor (1980) suggested a simple Clinitest technique for estimating reducing sugar content of potatoes. The technique was originally devised to test urine of diabetic patients. Louwes and Neele (1987) suggested the use of Reflockect Glucose test strips as an alternative to frying chips.

Recently, several good processing cultivars have been developed, some even with cold processing ability, but none appears to have a high and stable yielding ability comparable to the current high yielding maincrop cultivars. A review of the performance of the released chipping and french fry cultivars in the last decade would verify this point.

E. Tuber Defects

Defects such as second growth, knobiness, and germination result, at least in part, from susceptibility to stress (Gray and Hughes 1982). External growthcracks are associated with particular genotypes, and develop during periods of rapid growth. No special breeding activity is necessary

other than discarding such clones (Holden 1981). Probably a more significant problem is heat necrosis or internal brown spot. The primary cause is still undetermined (Iritani et al. 1984), and in areas where it is a problem breeders select against susceptible clones. Knowledge of other defects is more extensive.

1. Greening. Tuber greening may occur in the field through the tubers being produced on relatively long stolons or in a relatively high position on the plant. In a breeding program normal selection practices ensure these traits have minimal impact (Holden 1981).

Postharvest greening during storage in retail outlets is considerably more important (Gray and Hughes 1982). Holden (1981) raised the question whether strict limitation to light exposure or appropriate packaging were simpler ways to deal with this problem, but 10 years later there is still a considerable waste from greening. The potential for a breeding solution for the tuber greening problem has been demonstrated by Parfitt and Peloquin (1981). Using diploid breeding material they determined tuber greening to be quantitatively inherited, with broad sense heritability sufficiently large to permit effective selection. The magnitude of differences among European cultivars has been demonstrated by Brown and Riley (1976), and among North American cultivars by Reeves (1988). Reeves (1988) also considers ratings of external color, internal color, and depth of greening, and the effect of red and russet skin types on the extent of greening.

2. Mechanical damage. Damage is generally divided into two broad groups: (1) external damage including skinning or scuffing, splitting and shatter cracking, and (2) internal bruising or black spot which also includes pressure bruising during extended storage (Salunkhe et al. 1989). The control of mechanical damage is an important factor in marketing a potato crop, and a large component of that control is due to the cultivar (Ross 1986). Numerous tests have been developed to evaluate internal and external damage (Ross 1986), but for the most part these are better suited to studying the rheological properties of tubers than to screening breeding populations.

External damage has most recently been investigated by Skrobacki et al. (1989). De,Maine and Caligari (1988) found a drop test to be efficient and to correlate with damage occurring in the field, while De,Maine (1988) used a pendulum test to demonstrate that damage resistance was genetically determined in a series of 2x – 4x crosses. Abrasive peeling for the evaluation of internal blackspot was recommended by Pavek et al. (1985) for the screening of large numbers of clones in breeding programs.

While such results are encouraging, the breeding problems identified by Cole (1980) are still largely valid, namely: (1) the difficulty in early generation screening, (2) the limited availability of resistant parents, (3) the interactions between genotype and site and year, and (4) the production of maincrop cultivars that can be harvested before soil temperatures get too cold yet have yields equal to late maincrop cultivars. Most breeders, where possible, will use at least one resistant parent in each cross while avoiding more susceptible parents (Ross 1986), and selection for this trait will be in the later clonal generations (French and Bailey 1980).

3. Hollow heart. Hollow heart can be a major defect, and although it is influenced by many factors one of the most important is the cultivar (Rex and Mazza 1989). Although the frequency of hollow heart is often recorded in evaluation trials, and there is much information on management and hollow heart, the only work on the genetics of the trait appears to be that of Veilleux and Lauer (1981). They found a high GCA in both $4x - 4x$ and $4x - 2x$ crosses, but a high SCA in only some of the $4x - 4x$ crosses (see section III B.). They also confirmed a high positive correlation between tuber size and hollow heart. This is an easy trait to select against by cutting and observing larger size tubers during grading.

F. Breeding Implications

The challenge for the breeder is to combine the various utilization traits, along with production and protection traits, to produce a commercially acceptable cultivar. One of the characteristics of the potato as a crop is that in some countries the same cultivars are sold both in fresh and in processing markets. This imposes additional demands on the breeder since traits for both markets have to be incorporated into a single cultivar. Two other general factors should be noted. First, cultivars of varying maturity are required in most utilization groups. This results in accepting compromise values for some traits, especially in selecting relatively early maturing cultivars. Second, good storability is a trait of increasing importance so that shrinkage and sprouting can be minimized without the use of sprout inhibitors. Current concerns with chemical residues are increasing the importance of selecting for long dormancy. On the basis of the individual traits reviewed above, and with particular reference to Howard (1974), Gould and Plimpton (1985), Ross (1986), and Salunkhe et al. (1989), the requirements for the major market sectors are reviewed below.

Fresh market traits divide into two groups: those that are required to some degree in all cultivars, and those that are market specific. Neces-

sary in all cultivars are good texture and flavor, the absence of sloughing—though there is a range of acceptable quality—an attractive appearance including shallow eye depth, and very importantly a lack of enzymic browning and after-cooking darkening. Market or region specific traits include flesh color, skin color, skin russetting, and shape. Cultivars intended for tablestock markets for boiling or salad uses may be somewhat lower in dry matter content, moister in texture, completely resistant to sloughing, and highly resistant to after-cooking darkening. Cultivars intended for baking potatoes may be much drier and mealier in texture. A specialized sector of this market is for prepeeled potatoes. For this purpose the absence of enzymic browning is essential. A new tablestock market is for potatoes for microwaving, for which the general requirements for superior cultivars are not yet defined.

The largest sector of the processing market is for frozen french fries. This market has some very specific requirements, the first of which is that tubers must be large (over 275 g), long or oblong, and smooth, so that wastage in peeling and slicing is minimized. Such cultivars must have high dry matter and mealy texture. An aspect of this not usually mentioned is that the dry matter must be high throughout the tuber, that is the pith region should be narrow, and the dry matter differential between the pith and the cortex should be small. To obtain golden colored fries reducing sugars should be low, but need not be quite as low as for chipping cultivars.

Chip potato cultivars have specific requirements for round to oval shape, and generally uniform size up to about 75 mm diameter, to accomodate processing and packing of the finished product. Since oil content of chips can exceed 40% a high dry matter is essential to minimize oil uptake, and blistering, which also varies by cultivar, should be minimal. Consistently obtaining uniform, light colored chips is also essential so a very low reducing sugar content is critical. Sugar levels vary with storage conditions, but levels not exceeding 0.25% at the time of processing appear to be an appropriate breeding objective.

There are various types of dehydrated products. Cultivars are not bred specifically for this use, and important traits such as easy disintegration during cooking, little rupturing of cells, and specific starch characteristics, are not evaluated by breeders. Also important to maintain good color in dehydrated products are low reducing sugars and low after-cooking darkening.

Potatoes for canning must be round to oval, small (<35 mm), and must not slough or disintegrate, so low dry matter is required. Absence of after-cooking darkening is essential. The over-riding requirement for starch cultivars is a high dry matter content.

VI. PROTECTION TRAITS

A. Resistances to Diseases and Pests

The development and use of potato cultivars with pest and disease resistances is an objective of many breeding programs (Proudfoot 1976; Umaerus 1980; Mackay 1982; Erjefält 1986; Pavek 1987; Schöber and Schiessendoppler 1987; Świeżyński 1987; Tarn 1987; Wastie and Solomon 1988). It is unlikely that new cultivars with resistance to all potato pathogens can be developed (Thurston 1978; Mackay 1982), but cultivars with multiple resistances are being pursued (Proudfoot 1969; Mackay 1982; Prasad and Nagaich 1983; Sieczka 1989). Resistance mechanisms in the active, biochemical sense and physical modifications of the host that may entrap, exclude, or repel organisms are useful to the practical plant breeder (Russell 1978).

The concept of tolerance whereby plants may be infected yet exhibit minimal symptom expression or influence on growth is considered undesirable for viral diseases since symptomless plants may serve as foci of infection. In the case of early generation screens, this would necessitate maintaining separate stocks or indexing survivors to ensure freedom from disease (Plaisted et al. 1984). Tolerance to potato cyst nematodes is a useful accessory to true resistance because less nematocides are required (Wastie and Solomon 1988).

Increasing concern about the impact of pesticides on the environment and human health has emphasized the desirability of using inherent plant resistance to lessen the effects of disease. Pimentel and Levitan (1986) reported that 500 million kilograms of pesticides were used for agricultural purposes in the USA, and of this less than 0.1% reached the target. They estimated that for all crops the annual 3 billion dollars cost of pesticidal control resulted in increased yield worth 12 billion dollars countered against the 1 billion dollars in environmental and social costs of damages caused by pesticides. Andow and Davis (1989) reviewed the effects on food and the environment of intensified use of agricultural chemicals in the last four decades. Once developed, disease resistance does not add directly to the cost of production, except perhaps in higher costs for premium seed tubers (Wastie and Solomon 1988), and will permit regrowth of stock for seed. Fry and Tweedy (1983) expect losses from plant diseases to have a more critical influence on civilization in the next 20 years than was the case in the past several decades. Resistance is most effective when integrated with other control measures (Russell 1978; Dimock and Tingey 1985; Wastie and Solomon 1988). As Fry et al. (1983) have shown with late blight, small increments of improved resistances may permit fewer pesticide applications. It has been demon-

strated that a leafroll resistant cultivar requires less insecticide to lessen disease spread (Fry 1980).

The general principles of resistance breeding are similar to those of breeding for other traits. Helgeson (1989b) summarized the process as follows: identify the disease and the organism responsible, develop tests to assess resistance in breeding lines or wild species, breed resistances into lines, and select those with improved resistance. Johnson (1987) cites the interaction of two genetic systems as the major challenge of incorporating resistance as a character. There are several prerequisites which must be met before effective breeding for protection traits can be undertaken: a heritable trait, genetic variability for the trait, and the ability to distinguish between resistant and susceptible individuals. It must also be decided whether or not the desired protection can best be met by breeding (which is time consuming) or by some other means. The likelihood of achieving success by the various control methods must also be assessed before a breeding program for a specific protection trait is launched. When it is determined that breeding for resistance traits is feasible, priorities can be set. These will vary from region to region according to the occurrence and significance of local disease pressures.

Several approaches may be taken to increase disease resistance through a breeding effort. Mackay (1982) describes a two-tiered approach: firstly, parental line development and early generation screening, and secondly, the assessment of disease reactions in advanced lines and cultivars. The relative stage at which testing takes place depends on several factors including the quantity of plant material required, the reliability of the test, and the relative priority of the trait. When resistance to a particular disease is emphasized in a program, progress may be rapid (Mackay 1982). This will be influenced by accessibility of resistance traits and the mode of inheritance.

Determination of parental line reactions are useful for choosing parental combinations (section III B). These data can be augmented by progeny analyses (Tai and Hodgson 1975). Plaisted et al. (1984) and Świeżyński (1984) have reviewed the screening for disease resistances in early generations. Jellis, et al. (1987a) have outlined the screening for disease resistances at the Plant Breeding Institute in Cambridge, UK, and screening for insect resistance in early generations has been reviewed by Sanford et al. (1984). Selected references for screening methods are presented in Table 8.7.

In later generations, breeders need to select clones with improved resistances coupled with acceptable quality and horticultural traits. Conversely, programs often choose to eliminate advanced selections with extreme susceptibility to specific diseases (Russell 1978). To categorize reactions for cultivar descriptions and registrations, selections may be

Table 8.7. Protection traits: screening and assessment methods with selected references.

Disease Agent/Pest	Screening Methods	Assessment Methods
BACTERIA		
<i>Clavibacter michiganense</i> subsp. <i>sepedonicum</i> ¹ (Spieck & Kott.)	Manzer and McKenzie 1988; Zielke and Naumann 1987.	
<i>Erwinia carotovora</i> subsp. <i>atroseptica</i> (Van Hall) Dye	Jellis et al. 1987a; Lapwood and Read 1985; Ross 1986.	Bain and Pérombelon 1988; Bourne et al. 1981; Gans and Wooster 1987; Hossain and Logan 1983; Lapwood and Gans 1984; Lapwood et al. 1985; Lapwood and Read 1985, 1986; Lapwood et al. 1984; Logan 1985; Wastie 1984, 1987; Wastie and McKay 1985.
<i>E.c.</i> subsp. <i>carotovora</i> (Jones) Dye		
<i>Streptomyces scabies</i> (Thaxter) Waksman & Henrici	Bjor and Roer 1980; Caligari and Wastie 1985; Dykstra 1956; Jellis et al. 1987a; Langton 1972b; Lauer and Eide 1963; Loria and Kemper 1986; Plaisted et al. 1984; Ross 1986.	Dykstra 1956; Dowley 1972b; Gans and Wooster 1987; Gunn et al. 1983; Marais and Vorster 1988; Pfeffer and Effmert 1986; Schöber 1987b; Wale 1983.
FUNGI		
<i>Alternaria solani</i> Sorauer	Caligari and Nachmias 1988; Douglas and Pavek 1972; Frank et al. 1979; Reifschneider et al. 1985.	Pelletier and Fry 1989; Reifschneider et al. 1984; Schiessendoppler 1987.
<i>Fusarium</i> spp. ²	Bång 1984a; Behnke 1980; Bjor 1987a; Corsini and Pavek 1986; Götz 1980; Huamán et al. 1989; Jellis 1975; Jellis et al. 1987a; Radke and Escande 1975; Ross 1986; Wiersema 1977b.	Bång 1984b; Boyd 1952 a,b; Jellis and Starling 1983; Langerfeld 1987a; Leach and Webb 1981; Olsson 1989; Seppänen 1981; Wastie et al. 1989.
<i>Helminthosporium solani</i> Durieu & Mont.		Turkensteen 1987.
<i>Phoma foveata</i> ³ (Foister)	Bång 1984a; Bjor 1987a; Jellis 1982; Ross 1986; Wastie et al. 1988, 1990; Wiersema 1977a.	Bång 1984b; Copeland and Fox 1987; Gans and Wooster 1987; Jellis 1978, 1982; Langton 1971; Seppänen 1982; Wellving 1976.
<i>Phytophthora infestans</i> (Mont.) de Bary	<i>Foliage:</i> Caligari et al. 1984, 1985; Jellis et al. 1986; Lacey et al. 1987; Malcolmson and Killick 1980; Plaisted et al. 1984; Platt and Tai 1984; Ross 1986; Umaerus et al. 1983.	<i>Foliage:</i> Cruikshank et al. 1982; Garcia et al. 1977; Malcolmson 1976; Schöber 1987a; Stewart et al. 1983a; Stewart et al. 1983c; Tegera and Fouarge 1984; Umaerus 1987; Umaerus and Lihnell 1976.

Table 8.7. Continued.

Disease Agent/Pest	Screening Methods	Assessment Methods
	Tubers: Bjor 1987b; Howard et al. 1976; Langton 1972a; Ross 1986; Umaerus et al. 1983.	Tubers: Darsow 1987; Deahl et al. 1974; Gans and Wooster 1987; Stewart et al. 1983b; Tegera and Fouarge 1984.
<i>Polyscytulum pustulans</i> (Owen and Wakef.) Ellis		Carnegie and Cameron 1983; Førsund 1987c.
<i>Rhizoctonia solani</i> ^a Kühn	Buriticá and Velandia 1977; Frank et al. 1976; Frank and Wilson 1972; Ross 1986.	Banville 1974; Bolkan and Wenham 1973; Chand and Logan 1982; Dowley 1972a; Førsund 1987b; Frank et al. 1976; Leach et al. 1983; Little et al. 1988.
<i>Spongopora subterranea</i> (Wallr.) Lagerh.	Kirkham 1986; Manzer et al. 1964; Sampson 1983.	Gans et al. 1987; Gans and Wooster 1987; Jellis et al. 1987b; Winter 1987.
<i>Synchytrium endobioticum</i> (Schilb.) Perc.	Jellis et al. 1987a; Sharma and Cammack 1976; Ross 1986.	Langerfeld 1987b; Magnus 1987; Proudfoot 1976.
<i>Verticillium albo-atrum</i> Reinke & Berthier	Corsini et al. 1988; Nachmias et al. 1983; Platt and Sander-son 1987.	Busch 1966; Corsini et al. 1985; Davis et al. 1983; Hung and Whitney 1982; Nachmias and Krikun 1987; Susnoschi et al. 1976.

V. dahliae Kleb.

VIRUSES AND VIROIDS

PLRV (luteovirus)	Boulton et al. 1988; Butkiewicz and Dziewonska 1982; Chuquillanqui and Jones 1980; Davidson 1973; Davies et al. 1975; Jellis et al. 1987a; Ross 1977, 1986; Wiersema 1972.	Bagnall and Tai 1986b; Barker and Harrison 1984; Beekman 1987; Davies et al. 1975; Gans and Wooster 1987.
PVA (potyvirus)		Bagnall 1961; Beekman 1987; Dědíc 1979.
PVM (carlavirus)	Dziewonska 1986; Ross 1986.	
PVS (carlavirus)	Ross 1986; Zadina 1979.	Goth and Webb 1985.
PVX (potexvirus)	Jellis et al. 1987a; Plaisted et al. 1984; Ross 1977, 1986; Wiersema 1972.	Bagnall 1961; Beekman 1987.

Table 8.7. Continued.

Disease Agent/Pest	Screening Methods	Assessment Methods
PVY (potyvirus)	Boulton et al. 1988; Chrzanowska and Zagórska 1982; Davila and Fernandez- Northcote 1984; Jellis et al. 1986; Jellis et al. 1987a; Plaisted et al. 1984; Ross 1977, 1986; Wiersema 1972.	Bagnall and Tai 1986a; Beekman 1987; Davies et al. 1975; Gans and Wooster 1987; Singh and Somerville 1987.
PSTV		Pfannenstiel and Slack 1980.
TRV (tobro virus)		Harrison and Cooper 1974; Gans and Wooster 1987.
INSECTS⁵		
<i>Empoasca fabae</i> (Harris)	Radcliffe 1982; Sanford et al. 1984; Tarn 1987.	
<i>Leptinotarsa</i> <i>decemlineata</i> (Say)	Cantelo et al. 1987; Dimock and Tingey 1985; Radcliff 1982; Sanford et al. 1984; Tarn 1987.	
<i>Aulacorthum solani</i> (Kaltenbach)		Beekman 1987; Harrewijn 1986; Singh et al. 1983.
<i>Macrosiphum</i> <i>euphorbiae</i> (Thomas)		
<i>Mysus persicae</i> (Sulzer)		
NEMATODES		
<i>Globodera pallida</i> (Stone)	Hansen 1985; Lacey et al. 1987; Mugniery 1983; Phillips and Dale 1982; Phillips 1981; Phillips et al. 1988; Ross 1986.	Arntzen and Bakker 1988; Dale et al. 1988; Dellaert and Vinke 1987; Phillips and Trudgill 1985; Seinhorst 1984; Storey and Marks 1983.
<i>G. rostochiensis</i> (Woll.)	Hansen 1985; Plaisted et al. 1984; Ross 1986.	Arntzen and Bakker 1988; Brodie and Mai 1989; Seinhorst 1984.
<i>Meloidogyne</i> spp.	Jatala 1983; Plaisted et al. 1984.	

¹syn = *Corynebacterium sepeidonicum* (Speick. and Kott.) Skapt. and Burkh.

²common dry rots include:

F. sambucinum Fuckel. Perfect state: *Gibberella pulicaris* (Fr.:Fr.) Sacc.

F. solani (Mart.) Sacc. var. *coeruleum* (Lib. ex Sacc.) C. Booth.

F. sulphureum Schlechtend. (syn. *F. sambucinum* Fuckel f.6 Wollenw.) Perfect state: *G. cyanogena* (Desm.) Sacc.

³syn = *P. exigua* var. *foveata* (Foister) Boerema

⁴Perfect state—*Thanetophorus cucumeris* (Frank) Donk.

⁵see also Tingey 1986.

entered in disease evaluation trials conducted by breeding programs (Pavek 1987), by cooperating phytopathologists, or by independent agencies such as the National Institute of Agricultural Botany (NIAB) in the UK. Assessment techniques are devised with an understanding of the host, pathogen, and environmental interactions (Russell 1978), and standard scoring systems or keys have been published to aid assessments (James 1971; NIAB 1985; EAPR 1987) and frequently these provide illustrations to help estimate the surface area affected. Campbell and Duthie (1989) have provided sampling guidelines to improve the reliability of disease assessments. Selected references for assessment methods are presented in Table 8.7. Results of evaluations are published at intervals in serial publications (Stegemann and Schnick 1985; Wilcox 1989; RIVRO 1990). Data are frequently summarized on 5- or 9-point scales for easy interpretation and as an aid to computerized record keeping and retrieval, though scales vary from country to country in that high values may denote high resistance or, alternatively, high susceptibility. Comparisons of values can only be reliable with knowledge of the test methods used, the methods of calculating scores, and the control cultivars used for comparison (Førsund 1987a; Gans and Wooster 1987).

Several other strategies for improving disease resistance may hold promise. Matern and Strobel (1987) reviewed the potential for screening protoplasts and protoclonal lines with fungal pathotoxins (e.g., *Alternaria solani*), and Foroughi-Wehr et al. (1986) reported the results of screening calli and protoplasts with toxins from *P. infestans* and *Fusarium* spp. in order to increase the level of resistance in regenerants. Meulemans et al. (1987) reported the selection of resistance to *P. infestans* using dual in vitro cultures of plant and pathogen. Conditions to optimize infection of protoplasts with PVX (Prakash and Foxe 1985) and with PVY (Barker and Harrison 1984) have been described. Gunn et al. (1985) assessed resistance to scab in protoplast derived somaclones. The variability derived from somaclones or through mutation is useful for applied programs only when combined with powerful selection systems (Wenzel et al. 1984). The introduction of foreign genes into cultivars (Stiekema et al. 1988) has opened the possibility of transferring genes for resistance into susceptible cultivars.

The influences of beneficial and pathogenic organisms on or near the host as well as the interactions between pathogens on the expression of resistance have received some attention (Zink and Secor 1982; Zott and Janke 1983; Azad et al. 1987). The relationship between the nutritional status and physiological age of the host and resistance to disease-causing organisms has been recognized (Carnegie and Colhoun 1983; Conway 1989; Kelman et al. 1989; Pennypacker 1989).

1. Protection traits and the germplasm resource. Although most current North American and European cultivars have exotic germplasm sources in their pedigree (De Jong and Tarn 1984; Stegemann and Schnick 1985; Ross 1986; Hermesen 1989; Plaisted and Hoopes 1989), this is not necessarily an indication of a widespread use of germplasm. The costly and time-consuming development of adapted germplasm has resulted in the very heavy use of relatively few adapted germplasm resources. Ross (1986) lists 18 recently developed European cultivars in which the PVY immunity (conferred by the gene Ry_{sto}) can be traced back to a small number of *S. stoloniferum* accessions. Via adapted germplasm developed at the Max Planck Institute in Germany, this gene has been incorporated into a large number of cultivars around the world. Similar situations exist in the cases of resistance to several other pests. In most scab-resistant cultivars, the resistance can be traced back to the old German cultivar 'Richter's Jubel' and its progeny such as 'Hindenburg' (Frandsen 1958). 'Richter's Jubel' appears in the pedigree of 71% of the cultivars released in North America between 1956 and 1985 (Plaisted and Hoopes 1989). In many cultivars with resistance to pathotype Ro1 of the potato cyst nematode, this resistance can be traced back to a single dominant gene from the Commonwealth Potato Collection accession *S. tuberosum* ssp. *andigena* CPC 1673. This in turn was a collection of true seeds from the Bolivian Group Andigena cultivar 'Polo' (Plaisted and Hoopes 1989). The large number of cultivars in *S. demissum* cytoplasm (Section II, D.) is another example of the relatively limited use which has been made thus far of germplasm resources. The development of improved germplasm with a broader base for pest resistance is therefore warranted. Inventories of several gene banks provide information on the presence or absence of specific protection traits (Van Soest 1983b; Hanneman and Bamberg 1986; Hoekstra and Seidewitz 1987; Huamán 1987). The Inter-Regional Potato Introduction Project in the USA has recently initiated massive screening for a large number of protection traits (Hanneman 1989).

B. Bacterial Diseases

The expression of bacterial diseases of potatoes is favored in warm, moist environments. Apparently healthy seed tubers may harbor bacteria that will multiply rapidly when environmental conditions are suitable. Production of seed tubers in a flush through system will reduce the incidence of soft rots and blackleg, although stock may quickly become recontaminated since the bacteria are ubiquitous. There is zero tolerance for bacterial ring rot disease. Of the three genera of bacteria

dealt with here, common scab is considered the most promising candidate for breeding for resistance.

1. *Clavibacter michiganense* subsp. *sepedonicum* (syn. *Corynebacterium sepedonicum*) (Bacterial Ring Rot). There is considerable genetic variability for resistance to Bacterial Ring Rot (BRR) among cultivars, and this has been used in breeding for resistance (Frandsen 1958; Zielke and Naumann 1987). Immunity to BRR has, thus far, not been reported. In North America BRR represents a unique disease situation in that it is controlled by phytosanitation and extremely strict certification standards. Breeding for partial resistance may lead to cultivars which, even though they are infected, have a degree of resistance to the expression of typical field and tuber symptoms (Manzer and McKenzie 1988). Thus in North America the objective regarding BRR in most potato breeding programs is to produce susceptible cultivars which show typical symptoms when infected.

2. *Erwinia* spp. (Soft Rot and Blackleg). There are three *erwinias* which cause soft rot in potatoes: *E. carotovora* ssp. *carotovora* (Ecc), *E. carotovora* ssp. *atroseptica* (Eca), and *E. chrysanthemi* (Echr). The host range of Eca is restricted mostly to potatoes. Ecc has a wide distribution in both the temperate and tropical zones and also has a wide range of host plants (Pérombelon and Kelman 1980). Blackleg is primarily caused by Eca but can also be caused by Ecc (Langerfeld 1984a). Terminology for these diseases has been outlined by Pérombelon and Kelman (1987). Echr attacks a broad range of tropical and subtropical crops including potatoes. It has recently also been isolated in some cool temperate countries. There is genetic variability among cultivars for resistance to both soft rot and blackleg (Frandsen 1958; Wastie and Mackay 1985; Lyon 1989). There may be several mechanisms of resistance to soft rot. However, many aspects of these mechanisms are still poorly understood and require more investigation before the resistance genes can be accurately described (Lyon 1989). It is necessary to breed separately for soft rot and blackleg (Ross 1986). Several screening methods have been developed but methods suitable for use in early generations are still lacking (Logan 1985; Wastie and Mackay 1985). This has probably contributed to the fact that thus far, breeding for resistance to both black leg and soft rot has a relatively low priority in many breeding programs. A high level of resistance to soft rot has recently been transferred from *S. brevidens* to *S. tuberosum* via somatic hybridization (Austin et al. 1988).

3. *Streptomyces scabies* (Common Scab). Common scab is an

actinomycete of worldwide importance, especially in areas with a temperate climate. Resistance has been reviewed by Frandsen (1958), Alam (1972), and Ross (1986). The resistance in most of the current resistant cultivars can be traced back to 'Richter's Jubel' and its descendant 'Hindenburg' (Frandsen 1958). In a study of segregating tetraploid progenies, Krantz and Eide (1941) concluded that resistance was controlled by a single dominant gene. Subsequent studies on the diploid level have confirmed that the inheritance of scab resistance is relatively simple. Cipar and Lawrence (1972), in an analysis of haploids from two cultivars, suggested that scab resistance is controlled by more than one but probably no more than three loci. Alam (1972), in a study of diploid hybrids, concluded that at one locus a dominant allele confers resistance and that another locus confers scab resistance when it is in a homozygous recessive state. Pfeffer and Effmert (1985) have initiated the development of tetraploid parents which are homozygous for resistance to common scab. Evans et al. (1986) found an increase in scab resistance in explant-derived potato clones from the susceptible cultivar 'Désirée'.

C. Fungal Diseases

Turkensteen (1978) has listed 31 fungal pathogens of potato. Of these, five were considered of worldwide importance and an additional two were classified as having a worldwide distribution but a more-or-less local importance.

1. *Alternaria solani* (Early Blight). Harrison (1978a) has listed the countries reporting this as an economically important disease. Thus far, the major control method has been the use of fungicides, but considerable genetic variability for resistance is available among cultivars and germplasm (Douglas and Pavék 1972; Harrison 1978a; Reifschneider et al. 1986). A wide range of resistance is available among the primitive cultivated diploids (Herriott et al. 1986) and wild *Solanum* species (Hanneman 1989). The heritability for the transfer of resistance from the diploid to the tetraploid level is high (Herriott et al. 1990). It has been suggested that resistance to early blight may be related to the glycoalkaloid concentration in the leaves of aging plants (Sinden et al. 1973). Resistance also appears to be related to incubation period, lesion expansion, and sporulation rate (Pelletier and Fry 1989).

2. *Fusarium* spp. (Dry Rots). Many species of *Fusarium* cause dry rot in different areas of the world. The nomenclature and taxonomy of the genus is controversial, and several classification systems have been proposed. According to Booth's (1971) system of classification, 20 species

are pathogenic on potato tubers. The more commonly found dry rots in temperate climates are listed in the footnotes to Table 8.7.

In most temperate regions the dry rot fungi are mainly wound parasites and develop during storage. In warmer climates *F. eumartii* and *F. oxysporum* cause both wilting and tuber rot (Lapwood 1978). There is considerable genetic variability for resistance to dry rot among cultivars and advanced breeding clones (Leach and Webb 1981). Olsson (1989) has reviewed the biochemical and mechanical factors involved in the identification of resistance. This resistance tends to be species specific; specific genotypes often differ in their reaction to different *Fusarium* species (Frandsen 1958; Seppänen 1981; Corsini and Pavek 1986). The resistance to *F. eumartii* may be controlled by a single dominant gene (Escande and Radtke 1973). Corsini and Pavek (1986) reported that in *S. tuberosum* cultivars and advanced breeding clones, the resistance to *F. coeruleum* and *F. sambucinum* was under separate genetic control and highly heritable. Similarly, in a progeny analysis of several Group Andigena cultivars, the resistance to *F. oxysporum* Snyder and Hansen was found to be independent of resistance to *F. solani* Snyder and Hansen (Huamán et al. 1989). Jakubiec and Suska (1984) found a very high level of resistance to dry rot in several wild potato species and in their hybrids with *S. tuberosum* haploids. Behnke (1980) was able to select resistant callus which had been screened to the culture filtrate of *F. oxysporum*. Interactions between dry rot fungi and soft rot bacteria (*Erwinia* spp.) have been reported. A combined resistance to both dry rot and soft rot is desirable and has been found (Huamán et al. 1989). However, there does not appear to be any correlation between resistance to dry rot and soft rot pathogens (Corsini and Pavek 1986) and separate screening tests are recommended (Munzert and Hunnius 1980).

3. *Phoma foveata* (syn. *P. exigua* var. *foveata*) (Gangrene). Gangrene is a wound parasite causing serious storage disease in the UK (Boyd 1972; Jellis 1982). There are differences in susceptibility between cultivars (Boyd 1972; Wastie et al. 1988). Several screening methods for resistance have been developed (Table 8.7), and screening for resistance is now part of many European breeding programs (Lapwood 1978; Jellis 1982). Olsson (1989) has reviewed the biochemical and mechanical factors involved in resistance. The heritability of resistance appears to be high. Susceptibility tends to be dominant, and thus resistant individuals may possibly be found in progenies from susceptible parents (Wastie et al. 1988). A weaker parasite, *P. exigua* Desm. var. *exigua*, occurs in Europe and North America and causes a tuber disease called pocket rot.

4. *Phytophthora infestans* (Late Blight). The breeding for resistance to

late blight has recently been reviewed by Howard (1982), Ross (1986), Schöber (1987c), Thurston (1979), and Umaerus et al. (1983). One of the major problems in controlling *P. infestans* has been the ability of the fungus to develop new races to major genes for resistance on a gene-for-gene basis. Thus, the focus of breeding for resistance has switched from the unstable resistance conferred by major genes (vertical resistance) to the polygenically inherited field or horizontal resistance which tends to be stable (Vanderplank 1984; Simmonds and Wastie 1987). The concept of horizontal and vertical resistance has recently been criticized (Nelson 1978; Parlevliet 1979). According to Nelson (1978) residual effects of major genes after being overcome by corresponding races of the pathogen can still provide a relatively low level of resistance. An accumulation of such "defeated" genes may possibly provide a considerable level of horizontal resistance. As pointed out by Umaerus et al. (1983), for the breeder the important factor is the end result. Whether or not the components in the complex of characteristics leading to less disease can be properly labelled as one type of resistance or another is ultimately less important. The breeding for field resistance is more difficult and time-consuming than the incorporation of specific major (R) genes into cultivars. Field resistance is often associated with late maturity. This may be the result of the simultaneous transfer of both resistance and late maturity from the photoperiod unadapted sources of resistance (Howard 1970; Umaerus et al. 1983). Tai and Hodgson (1975) have developed a method to estimate the general combining ability of Group Tuberosum parents for field resistance. *Solanum demissum* is the major resistance source in most European cultivars. Other species which have contributed resistance to current cultivars include *S. tuberosum* ssp. *andigena*, *S. stoloniferum*, *S. vernei*, and *S. verrucosum* Schlecht. (Ross 1986). A large number of other wild tuber-bearing *Solanums* are reported to have resistance. Species with high levels of race non-specific resistance are concentrated in the Mexican and Bolivian-Argentinean parts of the centers of diversity of the potato (Van Soest et al. 1984). Since many wild *Solanum* species contain both major and minor genes for resistance, one of the first steps in breeding for a stable resistance is to distinguish between the two types of resistance. This is not always easy (Parlevliet 1983). A major gene conferring only partial resistance may have the same effect as the combined action of a group of minor genes. Test crosses may be necessary (Colon and Budding 1988). In order to maximize the total number of minor genes from various germplasm sources, Hermesen (1974) has proposed a system of column breeding (Section II. D. 4).

Thus far, most breeding for late blight resistance has focused on resistance in the foliage. There is also genetic variability for resistance in

tubers, but since there is no simple screening method for tuber resistance, this area has been neglected (Howard 1982). Resistance to foliar attack by the pathogen does not ensure resistance in the tubers, although reduced inoculum from the foliage minimizes tuber infection. Doster et al. (1989) reported that the initial appearance of foliage blight from infected tubers occurred earlier in susceptible cultivars than in cultivars with moderate resistance. Fungicides will continue to play a major role in the control of late blight even if cultivars with considerable foliar resistance are used (Platt 1987).

Phytophthora infestans is heterothallic, and two mating types, A1 and A2, are usually required to complete its sexual cycle. The A1 mating type is found throughout the world, but until recently the A2 type was believed to exist only in Mexico. The A2 mating type has now been found in many different countries, including several in the temperate zone (Shaw 1987). The implications of these findings are not yet clear. A better understanding of the genetics and the breeding system of the pathogen may lead to better methods of control, including breeding for resistance (Shaw 1987).

5. *Rhizoctonia solani* (Stemcanker and Black Scurf). *Rhizoctonia solani* infection of potatoes is one of the oldest and most widespread potato diseases in the world (Harrison 1978b). Thus far, little progress has been made in breeding for resistance. The heterokaryosis of the fungus has several implications for breeding for resistance. The great variability which this pathogen has demonstrated may require a polygenic type of resistance for control (Zachmann 1973). The evaluation of resistance is very complex since clones which appear resistant to one phase of the fungus may be susceptible to another phase (Harrison 1978b). Dowley (1972a) has classified cultivars on the basis of their apparent resistance to black scurf, but the evidence has been questioned by Banville (1987). In any case, resistance to black scurf is not necessarily resistance to stemcanker and vice versa. Nevertheless, when all phases of the attack by the pathogen are considered, there is still genetic variability for resistance among cultivars (Frank et al. 1976).

6. *Spongospora subterranea* (Powdery Scab). Powdery scab develops best under cool, moist conditions and is frequently associated with fields with poor drainage and irrigation (Gans et al. 1987). This fungus is a vector for potato mop-top virus (Hooker 1981). Among cultivars there is considerable genetic variability for resistance. 'Kennebec' is very susceptible (Manzer et al. 1964; Sampson 1983; Kirkham 1986); 'Nooksack' and 'Russet Burbank' appear to have a useful level of resistance (Sampson 1983; Kirkham 1986).

7. *Synchytrium endobioticum* (Wart). Wart was introduced into Europe from South America and since then has spread to many other parts of the world. It does not occur in continental North America. Most of the resistance breeding has been done in Europe. Agriculture Canada maintains a breeding program for wart resistance in Newfoundland as part of an integrated pest management program in order to protect the North American continent by reducing the inoculum level on this island (Hampson and Proudfoot 1974). Several factors have contributed to the general success story of wart control (Howard et al. 1969; Vanderplank 1984): breeding for resistance, legislation, and the fact that the spores of this soilborne organism are not dispersed by wind.

The inheritance of and breeding for wart resistance has been reviewed by Howard (1970) and Ross (1986). Langerfeld (1984b) has prepared a comprehensive literature survey of the causal agent. There are several races but there is no clear relationship between the genes for resistance in the several hosts and the races of the pathogen (Howard 1970). Resistance is usually due to one or two dominant genes, but other schemes have been hypothesized. Most studies on wart inheritance have been conducted with tetraploid parents. Future progress with the genetics of wart resistance may be possible with the use of diploids. The sources of resistance in current cultivars include Groups Tuberosum and Andigena as well as *S. acaule*. Although resistance is also found in several other wild species, the resistance already present in the cultivars is considered ample for the immediate future (Ross 1986).

8. *Verticillium* spp. (Verticillium Wilt). Verticillium wilt is of worldwide importance and is caused by the fungi *V. albo-atrum* and *V. dahliae*. The disease is especially severe in the western USA and Israel (Krikun and Orion 1979; Rowe 1985) and is the basic cause of the early dying disease complex (Rowe et al. 1987). Resistance to both *V. albo-atrum* and *V. dahliae* in *S. tuberosum* can be traced back to 'Katahdin' and 'Richter's Jubel' (Frandsen 1958; Krikun and Orion 1979; Davis 1985). High levels of resistance to *V. dahliae* have been found in several wild *Solanum* species (Corsini et al. 1988).

D. Viral Diseases

Since potatoes are commercially asexually propagated the crop is subject to heavy yield losses as a result of accumulating virus infections from one clonal generation to the next. Hooker (1981) lists 23 potato virus diseases of economic importance. Howard (1970) recognizes the following four types of plant virus resistance: tolerance, infection resis-

tance (or field resistance), hypersensitivity, and extreme resistance (or immunity).

Selection for tolerance is not advised (Wooster 1988). Field resistance seems to be controlled by polygenes. Crosses where both parents have a moderate degree of resistance may produce some progeny with a resistance higher than either of the parents. A parent with a very low level of field resistance will lower the resistance level in the progeny (Howard 1970). Ross (1983, 1986) has pioneered the development and use of germplasm with major gene resistance. He lists hypersensitive and extreme types of resistance to seven economically important viruses and 14 major genes which control them. Foxe and Prakash (1986) reported that the gene *Nx* is expressed in protoplasts, but this is disputed by Adams et al. (1986). There is no disagreement that the genes *Rx* and *Ry* are expressed in protoplasts (Barker and Harrison 1984; Adams et al. 1986). Little is known about the mechanisms of action of resistance genes (Barker and Harrison 1984).

Recently, transgenic plants have been produced in which coat protein genes of several viruses have been transferred to potato (Tumer et al. 1987; Hoekema et al. 1989; Kawchuk et al. 1989; Lawson et al. 1989). Although such plants may initially be resistant, it remains to be seen whether such resistance is permanent or whether these genes primarily cause a delay in symptom expression. If such plants can become infected with virus, the ability to detect the presence of the virus with the commonly used enzyme-linked immunosorbent assay (ELISA) method will be masked by the inserted coat protein genes.

1. Potato Leafroll Virus (PLRV). PLRV is a persistent aphid-transmitted virus. Resistance to PLRV is the result of a complex of several interacting factors including the host, the vector, and the virus (Bagnall 1977; Peters 1986; Barker 1987). The host resistance is field resistance (infection resistance) which appears to be controlled by many minor genes. Immunity or extreme resistance to PLRV is unknown (Howard 1982; Ross 1986). Hanneman (1989) lists six *Solanum* species as exceptional sources of resistance. *Solanum acaule* and *S. demissum* have, thus far, been the primary sources of resistance in many cultivars. Very promising sources of resistance have been found in *S. etuberosum* Lindl. and *S. brevidens* (Ross 1986), although these two species can only be crossed with *S. tuberosum* with difficulty (section II C 4). PLRV resistance has been transferred via sexual means from *S. etuberosum* to tuber-bearing *Solanums* (Chavez et al. 1988a). Resistance to PLRV and PVY has been transferred from *S. brevidens* to *S. tuberosum* via somatic hybridization (Gibson et al. 1988). The interaction of PVY and PVX reduces the levels of

resistance to PLRV infection in potatoes. It is therefore recommended that resistance to PVX and PVY be incorporated along with resistance to PLRV (Jayasinghe et al. 1989).

2. Potato Virus M (PVM). PVM is a non-persistent aphid-transmitted virus. Its main distribution is in Eastern Europe. In addition to field resistance two major genes for resistance are available, a dominant gene for hypersensitivity (Nm) from *S. megistacrolobum* Bitt., and a major gene for high resistance to infection (Gm) from *S. gourlayi* (Dziewonska 1986; Ross 1986).

3. Potato Virus S (PVS). PVS is transmitted through wound contact and, with some strains, by aphids as well (Ross 1986). Thus far two major genes for resistance are available, a dominant gene for hypersensitivity (Ns) derived from a Bolivian Andigena clone (Baerecke 1967), and a recessive gene originally found in the cultivar 'Saco' (Bagnall and Young 1972; Zadina 1979).

4. Potato Virus X (PVX). PVX is transmitted by wound contact. The strains of PVX can be divided into four groups (1 to 4) depending on their reactions with the genes for hypersensitivity (Nx and its allele Nb) and extreme resistance Rx (Ross 1986). The Nx and Rx genes for PVX resistance are similar to Ny and Ry for PVY resistance. The genes are frequently labelled according to their origin, for example Rx_{acl} from *S. acaule*. The genes Rx (derived from the primitive Chilean Group Tuberosum cultivar 'Villaroela'), Rx_{acl} (derived from *S. acaule*), and Rx_{adg} (derived from a progeny of Group Andigena CPC 1673) confer extreme resistance. Kishore and Rieman (1969) have reported a recessive type of immunity to PVX in *S. tuberosum*. The genes Nb, Nx, Rx, Rx_{acl} , and Rx_{adg} have been introduced into many cultivars (Ross 1986). Moreira et al. (1980) have reported a resistance-breaking strain, PVX_{HB}, from Bolivia. This strain overcomes Nb, Nx, Rx, Rx_{acl} , and Rx_{adg} . Also, strains which overcome gene Nx can easily be selected from common PVX strains. However, such strains were not widespread in stocks of field-immune cultivars. It has been suggested that resistance-breaking properties may be associated with other characteristics which have adverse effects on general fitness and ability to compete under conditions imposed by commercial agricultural practices (Adams et al. 1984). In a subsequent study, this hypothesis was not supported. Nevertheless, the probability of PVX strains which overcome Rx appearing spontaneously by mutation appears to be small (Jones 1985). Brown (1985) has reported a dominant gene for extreme resistance to strain PVX_{HB} in the wild Bolivian species

S. suurense Hawkes. This gene has already been incorporated into a fertile tetraploid gene pool which is completely crossable with Group Tuberosum cultivars (Brown 1985).

5. Potato Virus Y (PVY). PVY is a non-persistent aphid-transmitted virus. There are three groups of PVY strains: PVY^o, PVYⁿ, and PVY^c (Ross 1986). Field resistance has been used quite effectively in breeding for resistance to both PVY and PVA, especially in areas with a relatively low infection intensity (Bagnall and Tai 1986a). Two major genes are also used in breeding for resistance: Ny and Ry. Each of these two genes may have several alleles (Cockerham 1970). The Ny genes control a necrogenic reaction. They have been found in *S. tuberosum* Group Tuberosum, *S. chacoense*, *S. microdontum* Bitt., and *S. demissum* (Cockerham 1970). The reaction of some Ny genes depends on the virus strain, while other Ny genes apparently cover all strains. The Ry genes control extreme resistance (immunity) to all known strains of both PVY and PVA. Sources of Ry genes include *S. tuberosum* Group Andigena, *S. demissum*, *S. hougasii* Corr., and *S. stoloniferum* (Cockerham 1970; Beekman 1987). The most commonly used Ry genes are Ry_{sto} and Ry_{adg}. Screening for extreme resistance to both PVY and PVX can be done in the seedling stage (Ross 1986).

6. Potato Spindle Tuber Viroid (PSTV). PSTV is seed-transmitted which makes it a particular concern of potato breeding programs (Grasmick and Slack 1985; Singh et al. 1988). Sensitive detection methods such as polyacrylamide gel electrophoresis (Schumacher et al. 1986; Singh and Boucher 1988) and nucleic acid hybridization tests (Owens and Diner 1981) which are available commercially (Agdia Inc., Elkhart, IN) have permitted large-scale testing of breeding stocks. Parents used for crosses are routinely monitored for freedom from PSTV, as are subsequent field generations.

There is zero tolerance for PSTV in most seed certification programs, and for this reason PSTV is rarely a problem in commercial fields in North America (Singh 1986). Consequently, in countries with comprehensive seed production systems, the development of cultivars with resistance is not considered a priority.

Although resistant potato cultivars have not been identified, the extent of symptom expression has been shown to vary (Pfannenstiel and Slack 1980). Several PSTV strains exist which influence the extent of symptom expression. *Solanum* species have been screened for a source of resistance (Singh and Slack 1984), and recently transgenic 'Russet Burbank' plants exhibited cross protection to challenge inoculation by PSTV (Laksham et al. 1990).

E. Insects

Radcliffe (1982) has reviewed the insect pests of potato. The breeding for insect resistance including resistance to the Colorado potato beetle, potato leaf hopper, and aphids has recently been reviewed by Tarn (1987) and Tingey (1981). Tingey (1986) has reviewed the techniques for evaluating plant resistance to insects. There are at least two general mechanisms of resistance which can be used for control of more than one insect pest.

Potato glycoalkaloids have adverse effects on the behavior and developmental biology of the Colorado potato beetle and potato leafhopper, but glycoalkaloids are apparently not involved in aphid resistance (Radcliffe 1982). Early efforts in breeding for insect resistance in potato focused on resistance based on total glycoalkaloids (TGA) in the foliage. A major disadvantage of this mechanism is that the levels of TGA in the foliage are highly correlated with those in the tubers. It may be possible to find clones with high TGA levels in the foliage and safe levels in the tubers (Sinden et al. 1980), but a constant monitoring for TGA levels in the tubers of wild parents and resistant progenies is required (Van Gelder et al. 1988). The idea of basing resistance on TGA has now largely been abandoned in favor of resistance based on specific glycoalkaloids in the foliage (Sinden et al. 1980; Sanford et al. 1984; Tingey 1984; Tarn 1987). This allows the level of TGA to be reduced while maintaining or even increasing the level of resistance. The genetic and environmental control of potato glycoalkaloids has been reviewed by Sinden et al. (1984).

Glandular trichomes provide a physicochemical defense mechanism effective against several small-bodied insects such as leafhoppers and aphids. *Solanum berthaultii* Hawkes and other Bolivian species have been good sources of glandular trichomes (Sanford et al. 1984; Gregory et al. 1986; Tarn 1987). *Solanum berthaultii* has two types of glandular trichomes: type A is a short trichome with a four-lobed membrane-bound gland at its apex, while type B is a longer, simple trichome with an ovoid gland at its tip which continuously exudes a viscous exudate. An insect landing on the foliage is coated with exudate from the type B trichome and becomes agitated. The struggling insect disrupts the heads of type A trichomes which eventually results in a quinone formation, insect immobilisation, cessation of feeding, and death (Gregory et al. 1986). This resistance mechanism should be handled by breeders as a quantitatively inherited trait (Mehlenbacher et al. 1983, 1984).

1. *Empoasca fabae* (Potato Leafhopper). Potato leafhoppers (PLH) are of greatest economic importance in North America where they are associated with hopperburn, a physiological condition resulting from PLH feeding. Field resistance to *E. fabae* has been reported, but the resistance

factors have not been identified and the level of foliage resistance is generally low (Tarn 1987). Nevertheless, Sanford and Ladd (1987a) were able to increase the level of PLH resistance considerably after practicing recurrent selection in a population of Group Tuberosum. The most advanced recurrent selection populations should be good germplasm sources of PLH resistance for cultivar development (Sanford and Ladd 1987b). The importance of this pest led to the establishment in 1934 of a program in the USA to breed for resistance (Sleesman and Stevenson 1941), and at least one PLH-resistant cultivar, 'Sequoia', was released at that time (Gardner et al. 1945). A high degree of resistance to *E. fabae* has been found in many wild *Solanum* species (Radcliffe and Lauer 1968; Tarn 1987). In many of the most resistance species, the resistance is correlated with a high glycoalkaloid content in the foliage. The resistance in *S. berthaultii* may be an exception since the resistance mechanism appears to be in the glandular trichomes. *Solanum berthaultii* is a promising source of resistance (Sanford et al. 1984; Tingey and Laubengayer 1986).

2. *Leptinotarsa decemlineata* (Colorado Potato Beetle). The Colorado potato beetle (CPB) is the most important defoliating insect of the potato. It has an enormous adaptability. From a presumed origin in Mexico, it has successfully colonized areas between 15° and 55°N in North America and 35° to 60°N in continental Europe (Hsiao 1985). It has rapidly developed resistance to nearly all available potato insecticides in the northeastern USA where it is of particular economic importance.

It is generally considered that *S. tuberosum* does not contain any genes for resistance to CPB. Considerable resistance is available in the wild *Solanum* species (Torka 1958; Dimock and Tingey 1985; Tarn 1987). Utilization of CPB resistance based on *S. berthaultii* was initiated by the Cornell University potato breeding program in 1977, and progress has been made in transferring the resistance into advanced hybrids. Of concern is the report by Groden and Casagrande (1986) that the CPB may be able to adapt rapidly to the resistance conferred by *S. berthaultii*. Neal et al. (1989) studied the mechanisms of resistance to CPB in *S. berthaultii*. They concluded that "... the presence of type A trichomes is a fundamental requirement for expression of *S. berthaultii* resistance to L1 *L. decemlineata*. Type B droplets containing sucrose esters increase the expression of resistance in the presence of defensively active type A trichomes." Even a relatively low level of resistance may be of considerable value if incorporated into an integrated pest management program (Ferro 1985).

3. *Myzus persicae*, *Macrosiphum euphorbiae*, *Aulacorthum solani* (Aphids). In the temperate zone, the major damage to the potato crop by aphids is as vectors of virus diseases (Maramorosch 1980). They are vectors of the main persistent virus (PLRV) as well as of several non-persistent viruses, of which PVY is a major one. The development of aphid-resistant cultivars in order to control virus diseases has been a controversial subject. There are two general schools of thought with only a limited amount of evidence for each. One view is expressed by Adams (1975), who argued that the significance of aphid resistance in a potato crop is at least two-fold: (1) lessened aphid feeding and dispersal, and (2) reduced inoculation of aphid-borne viruses into healthy plants. The other view is that an increased resistance to aphids will cause a greater movement of the aphids in the crop and thus increase the spread of virus. This view is supported by the results of Baerecke (1958) and by Oertel et al. (cited by Beekman 1987). Arenz (cited by Gibson and Plumb 1977) found that *M. persicae* multiplied more rapidly on plants with PLRV than on ones with severe PVY and more rapidly on infected aphid-resistant than on healthy susceptible plants. Mndolwa et al. (1984) found no apparent direct relationship between colonization by *M. persicae* and resistance to PLRV and concluded similarly to Baerecke (1958) that breeding for resistance to green peach aphid colonization may not be as promising for PLRV control as developing PLRV resistant cultivars.

Gunenc and Gibson (1980) reported that the presence of glandular trichomes decreased multiplication of *M. persicae*, lessened probing, and lessened acquisition of PVY. Rizvi and Raman (1983) studied the effect of glandular trichomes from *S. berthaultii* on the spread of both PVY and PLRV in the field. Neither type A nor type B hairs had any effect on PVY spread, but the spread of PLRV was reduced significantly by type B hairs. Lapointe et al. (1987) reported that PVY acquisition from and transmission to *S. berthaultii* by *M. persicae* is reduced compared with *S. tuberosum*.

Kennedy (1976) concluded that "the effect of a vector-resistant cultivar on virus spread will depend upon the type of resistance (non-preference, antibiosis, or tolerance), the level of resistance, the relative importance of primary and secondary virus spread, the length of the acquisition, inoculation, retention, and latent periods of the virus, and the effect of virus infection on vector resistance in the plant." The glandular trichome mechanism of resistance from species such as *S. berthaultii* appears promising. Other sources of aphid resistance, not based on glandular trichomes, have been identified (Radcliffe 1982). A greater understanding of the relationships among host plants, vectors, and viruses are probably required before much progress can be made in virus control via aphid resistance.

F. Nematodes

Mai et al. (1981) list 38 nematode pests of the cultivated potato. Some nematodes can, in combination with other pathogens, produce a synergistic affect. The result may be a more rapid development of disease symptoms.

1. *Globodera rostochiensis* and *G. pallida* (Potato Cyst Nematodes). The center of diversity or origin of potato cyst nematodes is generally believed to be the Andean part of the Peru-Bolivia-Argentina triangle (Van Soest et al. 1983b). They were probably introduced into Europe in the second half of the 19th century along with potato collections which were brought in for purposes of breeding for resistance to late blight (Winslow 1978; Brodie and Mai 1989). Potato cyst nematodes (*G. rostochiensis*, pathotype Ro1) were probably introduced into the USA from Europe on returning military equipment after World War I. Potato cyst nematodes have been reported in at least 48 countries (Brodie and Mai 1989) and represent one of the most serious pests in potato production in Europe and the Andean region of South America. Many countries have strict quarantine regulations to prevent introduction and/or further spread.

Thus far five pathotypes have been reported for *G. rostochiensis* (Ro1 to Ro5) and at least four (Pa1 to Pa4) for *G. pallida*. The pathotype classification used here is that of Kort et al. (1977). Canto Saenz and Mayer de Scurrah (1977) have developed a new classification in order to include the additional pathotypes which have been found in South America. The classification of potato cyst nematodes is currently under review (Trudgill 1985). Resistance to potato cyst nematodes has been found in a large number of *Solanum* species (Dellaert and Hoekstra 1987; Chavez et al. 1988b; Dellaert et al. 1988; Jackson et al. 1988; Mayer de Scurrah and Van der Wal 1988). The resistant species have their distribution primarily in the Andes (Van Soest et al. 1983b). Resistance to potato cyst nematodes was not present in potato cultivars of the temperature zone before 1950.

The breeding for resistance to *G. rostochiensis* is primarily based on major genes, but minor genes can modify the resistance. The gene *H1*, originally found in Andigena CPC 1673 (see section VI A 1), confers a very high degree of resistance to pathotypes Ro1 and Ro4. This gene is now present in more than 60 cultivars in West Germany (Ross 1986) and has been used worldwide for developing cultivars with resistance to Ro1 (Brodie and Mai 1989). The *H1* gene does not confer resistance to *G. pallida*. There are at least two major genes for resistance to Ro1 in *S. vernei* hybrids. One of these appears to be at the same locus as *H1* (Mayer de Scurrah et al. 1973). Three major genes from *S. spegazzinii* Bitt. have

been identified: *Fa* conferring resistance to Ro1 and Ro2 but not to Ro5, *Fb* to Ro1 as far as Ro5, and *Fc* to some pathotypes of both *G. rostochiensis* and *G. pallida*. Ross (1986) concludes that breeding for resistance to *G. rostochiensis* pathotypes occurring in Europe has been solved. However, resistance to major genes has been broken, and a gene-for-gene relationship has been determined (Jones et al. 1981; Stone 1987).

Breeding for resistance to *G. pallida* has been difficult. The resistance to *G. pallida* derived from *S. vernei* differs from the qualitative resistance to *G. rostochiensis* conferred by the *H1* gene. The progenies derived from *S. vernei* hybrids do not exhibit a clear-cut distinction between resistant and susceptible. It was initially considered that the resistance to *G. pallida* from *S. vernei* was quantitatively inherited and was horizontal. However, it was subsequently discovered that some *S. vernei*-derived clones can be used as differential hosts to distinguish pathotypes. It has been suggested that this resistance is due to at least three major genes (Jones et al. 1981). A search is in progress for horizontal resistance to *G. pallida* (Dellaert et al. 1988). It is difficult to distinguish between genotypes with a polygenic horizontal resistance and those with major gene (vertical) resistance. Various nematode populations within the same pathotype may have different frequencies of virulence genes. Some major genes may have incomplete dominance (Dellaert and Hoekstra 1987). The British Neo-Tuberosum population contains considerable resistance to both *G. pallida* and *G. rostochiensis*. The resistance to *G. pallida* in this material resembles the resistance based on *S. vernei* (Glendinning and Phillips 1988). The stability which the *H1* gene has exhibited may be partly due to an apparent difference between field populations of *G. rostochiensis* and *G. pallida*. It appears that *G. pallida* pathotypes have a greater heterogeneity for virulence genes than *G. rostochiensis* (Turner et al. 1983). There are considerable differences in the number of cysts formed by both *G. rostochiensis* and *G. pallida* on "susceptible" *S. tuberosum* (including Group Phureja) clones. Such partial resistance may be a valuable source of horizontal resistance. It is conceivable that by further selection and breeding, advanced material with a higher level of horizontal resistance may be obtained (Arntzen and Wouters 1989). Several authors have used various ploidy manipulations with cultivated diploids which exhibited partial resistance to *G. pallida* (Langton and Ross 1982; Uhrig 1985a; De, Maine et al. 1986).

In addition to breeding for resistance and partial resistance, breeding for tolerance has been proposed. This is a more complex characteristic than resistance and consequently a more difficult breeding objective (Dale 1989).

2. *Meloidogyne* spp. (Root Knot Nematodes). Root knot nematodes are

widely distributed around the world, but since they occur primarily in areas where the soil temperature is 20°C or higher they are not a major general pest in the temperate zone. The degree and frequency of resistance to root knot nematodes is generally low in cultivars, but resistance is available in several wild tuber-bearing *Solanum* species (Madamba 1978). The mechanisms of resistance to root knot nematodes have been reviewed by Huang (1985). Resistance to root knot nematodes from diploid species has, via meiotic mutants, been transferred from the diploid to the tetraploid level (Iwanaga et al. 1989). At least two species occur in North America: the northern root knot nematode, *M. hapla*, and the Columbia root knot nematode, *M. chitwoodi*. These two species can survive soil temperatures to and below 0°C (Van Gundy 1985). Hoyman (1974) found a considerable genetic variability for resistance to *M. hapla* among *S. tuberosum* clones and a very high degree of resistance to *M. hapla* in several wild tuber-bearing *Solanum* species. Resistance to *M. hapla* is also available in *S. tuberosum* Group Andigena (Brodie 1984).

3. *Pratylenchus* spp. (Root Lesion Nematodes). At least 15 species of *Pratylenchus* have been reported associated with potato culture. *Pratylenchus penetrans* is an important potato pest in Europe and is also the most important nematode parasite of potatoes in the northeastern USA and Canada. (Brodie 1984; Kimpinski and Olthof 1987). Although resistance to *Pratylenchus* spp. has been reported in some commercial cultivars and in the wild diploid *S. sparsipilum* (Bitt.) Juz. et Buk., little effort has been made to exploit this resistance (Brodie 1984).

G. Herbicide Resistance/Tolerance

The terms herbicide resistance and tolerance have been described by LeBaron and Gressel (1983). Tolerance usually refers to relatively minor or gradual differences in intraspecific variability. Resistance is the maximum tolerance that can be achieved. Breeding for herbicide tolerance and/or resistance can be somewhat controversial. Faulkner (1982) has presented the case for breeding herbicide-tolerant crop cultivars. De Jong (1983) has argued that breeding for herbicide tolerance may be an oversimplification of a complex problem and that research on the development of new herbicides should be closely integrated with research on the development of new cultivars. Another factor to be considered in breeding for herbicide resistance is the possible yield reduction which may be inherent in resistant genotypes. For example, triazine resistance is associated with a minor modification of chloroplast proteins involved in photosynthesis which in turn affects the flow of electrons during photosynthesis. Triazine resistant rapeseed produces a lower yield.

than "normal" (susceptible) rapeseed (Forcella 1987; Oxtoby and Hughes 1989).

One of the currently most widely used herbicides in potatoes is metribuzin. Considerable genetic variability for metribuzin tolerance has been found among cultivars (Friesen and Wall 1984). Several methods of screening for metribuzin tolerance in potato have been described. In cultivated diploid potatoes the tolerance of metribuzin is controlled by a single nuclear gene (De Jong 1983). Considerable information about the mechanism of metribuzin tolerance in potato is available (Gawronski et al. 1986).

Recent advances in genetic engineering have provided a powerful new technology that can make possible rapid development of herbicide-tolerances in existing cultivars (Goodman 1987). Herbicide-tolerant regenerates of potato have been obtained by Wersuhn et al. (1987). Somatic hybridization between atrazine-resistant biotypes of *S. nigrum* L. and *S. tuberosum* have been produced by Gressel et al. (1984). Transgenic potato cultivars have reached the stage of field testing and, in initial trials, were found to be resistant to commercial doses of glufosinate (De Greef et al. 1989). Herbicide resistance and/or tolerance can be used as a screening technique to detect hybrids in somatic fusion experiments (Binding et al. 1982).

H. Gaseous Pollution Sensitivity

On a species basis, potatoes are considered tolerant to sulfur dioxide and hydrogen fluoride, moderately tolerant to nitrogen oxides, and sensitive to ozone (Ormrod et al. 1987). As these authors point out, cultivars may vary greatly in sensitivity, which is influenced by temperature, irradiation, water, and nutrition. In addition, plant responses may be modified by disease, growth regulators, and other pollutants. De Vos et al. (1983) compared controlled exposures to O_3 with ambient exposures in the field for 26 cultivars. The laboratory screening identified resistance to oxidants that remained effective over a range of field environments. Heagle (1989) has reviewed the influence of O_3 on crop yield.

VII. IN VITRO TRAITS

Tissue culture propagation of potato can be used extensively in a breeding program. Although some genetic material can be maintained as true seed, clonal material demands more labor-intensive methods. A disease-tested germplasm bank is greatly facilitated by maintaining nuclear stock in culture (Dodds 1988). Material conserved in culture has

little chance of becoming reinfected with disease-causing organisms. Access is available at any time of the year, and work can be scheduled to accommodate field work and other program requirements.

In northern and southern temperate regions the daylength during the growing season may be too long to permit many species to tuberize efficiently. In vitro storage therefore offers an alternative method of propagation. Exchange of breeding lines and clonal material is facilitated by shipping material in culture (Seabrook and Coleman 1988). Certification programs in many parts of the world require potato material to enter the systems as tissue cultured plantlets (Johansen et al. 1984). Micropropagation is a considerable advantage to quarantine authorities (Australian Plant Quarantine Service 1983; Miller-Jones and Howell 1986) because the plants are free of all soil.

Genotypic differences in reaction to culture conditions have been reported (Caligari and Powell 1989; Powell et al. 1989). Furthermore, the media employed in the culture regime affects the productivity of single-node cuttings used for micropropagation (Amirouche et al. 1985).

A. Regeneration

Shoots can be regenerated from a wide variety of tissues in the potato (Webb and Henshaw 1982; Espinoza and Dodds 1985; Uhrig 1985b; Wheeler et al. 1985; Rietveld et al. 1987; Preťová and Dedičová 1990). Regeneration of shoots from various explanted cultured tissues of potato has been considerably easier in some cultivars than others. This has been shown in studies of regeneration from anther cultures (Irikura 1975; Uhrig 1985b; Sonnino et al. 1989), leaf disks (Webb and Henshaw 1982), and stem internode sections (Wheeler et al. 1985). Chandra et al. (1985) reported the regeneration of shoots from stem sections of haploid but not from tetraploid genotypes of potato. Haploid progeny obtained via a haploid inducer, *S. phureja*, regenerated more readily than their tetraploid parents (Fish and Jones 1988). Similar results were obtained when haploid clones were compared with their tetraploid parents for resistance to *P. infestans* (De, Maine 1982) and *G. pallida* (De, Maine 1978; De, Maine et al. 1986). Regeneration of shoots from cultured roots has also indicated that not all cultivars are responsive to culture conditions (Espinoza and Dodds 1985). Several authors have suggested that the ability to regenerate from pollen be included in breeding lines (Cappadocia et al. 1984; Sonnino et al. 1989). Even in a regenerative genotype not all excised tissues are responsive (Quraishi and John 1985).

The precise mechanism of the genetic control of regeneration has not been reported except for anther culture (Sonnino et al. 1989). Before implementing breeding plans to include regeneration ability into new cul-

tivars, experiments outlining the heritability of regeneration will have to be conducted.

Lam (1975) and Upadhyia et al. (1982) reported the presence of globular somatic embryos in cultures of somatic tissue of potato. Recently, Preťová and Dedičová (1990) reported the regeneration of somatic embryos from immature zygotic embryos of 'Désirée' plants which had been selfed. Zygotic embryos which had not curved back on themselves were responsive to in vitro protocols. Preťová and Dedičová (1990) used a culture medium with 5% sucrose. Other researchers have noted a higher-than-usual requirement for sucrose during in vitro development of potato (Lawrence and Barker 1963; Seabrook and Douglass 1990). Gametophytic embryos have been reported from anther cultures of potato (Dunwell and Sunderland 1973; Irikura 1975; Sopory et al. 1978). If artificially-coated somatic embryos of commercial potato cultivars could be produced routinely, the potential for clonal seed would be considerable (O'Hair et al. 1987).

B. Maintenance of Disease-causing Organisms

The maintenance of specific strains of disease-causing organisms for testing the resistance of breeding lines is easily accomplished in vitro (Schenk and Neitzel 1985; Singh et al. 1988), and many seed testing laboratories now maintain a bank of potato cultures containing certain diseases. A disease positive culture repository is an efficient source of diseased material as checks for testing (McMorran and Allen 1983; Arndt and Schenk 1989). Maintaining positive disease checks in vitro also reduces the risk of cross-infection and contamination.

C. Apomixis

True seed production has not provided a uniform crop for highly developed regions. However, Hermesen (1980) proposed an experimental investigation into the induction of apomixis in cultivated potato germplasm. The aim was the production of genetically uniform true seed. Apomixis has only rarely been observed in potato (Hermesen 1980), and an extensive program of induced mutagenesis or "hit and miss" searches of germplasm would be required.

VIII. CULTIVAR RELEASE

As potato breeding has become increasingly scientific and expensive, legal protection of cultivars has been provided to enable breeders to

recover the cost of cultivar development. A landmark in such protection was the International Convention on the Protection of Plant Varieties (UPOV) signed in 1961, and to which 17 countries are now members (Mastenbroek 1988). In the USA patent legislation is also available for the protection of plant cultivars (Williams 1984), although the country is also a member of UPOV. Several USA potato cultivars are now protected by utility patents. Internationally, UPOV has had great significance in establishing the requirements for cultivar recognition. Details of requirements for performance assessment and procedures for cultivar registration, release, or listing vary with country and are not dealt with in this review, but several issues of general importance are considered.

A. Distinctness

Under the UPOV guidelines distinctness, uniformity and stability are required for cultivar recognition, along with novelty and name. Probably the most widely used guidelines for the morphological description of potato cultivars are those of UPOV (1986), which include 50 descriptors. These guidelines put considerable emphasis on lightsprouts (12 descriptors) using the methodology described by Houwing et al. (1986). The guidelines recommended by the Potato Association of America for North American cultivars (Anon 1983) are much less precise.

The minimum difference between two cultivars is an artificial concept (Schneider 1986) and is being challenged by the genetic manipulations of new biotechnology methods. Electrophoresis is a useful tool for distinguishing vegetatively propagated cultivars (Gilliland 1989) and has been used extensively in the potato (e.g., Stegemann and Loeschke 1976), but even this will be inadequate to separate cultivars with single gene differences that can be created using genetic engineering techniques. This latter situation can at present only be resolved with the use of restriction fragment length polymorphisms (RFLPs) as demonstrated by Gebhardt et al. (1989).

B. Uniformity and Stability

The UPOV requirements for uniformity and stability are very closely linked in a vegetatively propagated crop such as the potato which has been considered both uniform and stable except for the appearance of spontaneous mutations. However, with the widespread adoption of micropropagation methods, stability has become a more important issue.

The genetic instability of regenerants from tissue cultures of potato is well documented (Cassells 1985; Sree Ramulu et al. 1986; Sree Ramulu et al. 1989). Of concern to a breeding program is the stability of cultivars

during routine micropropagation. There is some evidence that unstable, chimerical cultivars such as 'Golden Wonder' are progressively more unstable as the stress of various tissue culture regimes is applied (Cassells et al. 1986). Ancora and Sonnino (1987) reported different levels of instability exhibited by regenerants from different parts of the potato plant. Long-term, single-node cuttings cultures of potato show decreased vigor in some cultivars (J. E. A. Seabrook, unpublished).

Data from true seed storage experiments with several plants indicate that genetic instability increases with age (Roos 1980). Because minimal growth conditions apply stress to tissues, cultures of vegetatively propagated plants like the potato kept in storage over long periods of time may be subject to some genetic change (Snowcroft 1984). Inadvertent selection pressure may therefore be applied to cultured tissues. Potato propagation laboratories should therefore plan on transferring tissues regularly, and frequently monitor in vitro maintained collections in the field.

Differences in isoenzyme patterns have been used to distinguish between potato cultivars for some time (Oliver and Martínez-Zapater 1984, 1985; Desborough 1985). However, spontaneous mutants such as 'Russet Burbank' had isoenzyme patterns identical to the parent clone 'Burbank' (Douches et al. 1989). Molecular markers offer opportunities to delineate single gene differences among regenerants, and to elucidate relationships among potato accessions in germplasm collections. RFLPs offer the opportunity to detect differences between phenotypic and genotypic effects (Ainsworth and Sharp 1989). Linkage maps for *S. tuberosum* have recently become available (Gebhardt et al. 1989), and some linkages among isoenzymes have been reported (Douches and Quiros 1987).

RFLPs directly characterize the genotype rather than the phenotype (Gebhardt et al. 1989), and this is an advantage over more conventional markers such as isoenzymes. Furthermore, as many RFLP markers can be mapped as there are molecular differences between genotypes (Gebhardt et al. 1989).

The value of planting genetically engineered material in the field as a way of assessing stability should not be underestimated. Although there appear to be no reasons to change the assessment criteria from those used for cultivars developed by traditional means (Maryanski 1988), in some situations special procedures have been followed in conducting such trials (Dale and Flavell 1988). Experienced seedsmen know the crops they work with and can offer invaluable appraisals of questionable material exposed to different growing conditions. Botanically conservative morphological characteristics such as sprout and flower morphology used for cultivar descriptions (UPOV 1986) should also be used when

monitoring for genetic changes in material regenerated from tissue culture.

C. Availability of Seedstock

Most potato production systems operate on a limited generation flush-through system for the production of seed tubers. Formal requirements for the virus-free entry of new cultivars into such systems can produce a bottleneck in the availability of seed. However, this can be overcome by the use of micropropagation to rapidly increase material for entry into certification programs (Matthews et al. 1986; Wilson et al. 1986; Bryan 1988). In North America promising selections from breeding programs have been placed in the virus-free program operated by Agriculture Canada since 1968 (Mellor and Stace-Smith 1987; Wright 1988). Rapid propagation can also accelerate seed production for cultivar trials (Wang 1985; Wooster 1986).

Although some new equipment such as laminar flow hoods and microscopes are necessary for micropropagation (Kyte 1987), many institutions with breeding programs also have tissue culture specialists or plant physiologists available for advice and with whom equipment can be shared. The training for micropropagation is simple, and technical staff used to working with breeding techniques such as hand pollination and cytology should have little difficulty learning new techniques. Principles of operation for any germplasm collection such as checking for mix-ups and monitoring for disease are also important in a tissue culture collection.

D. Management Profiles

Potato cultivars vary widely in production traits such as response to fertilizer, cultivar maturity, and tuber set and sizing behavior. There are also widely different requirements for a cultivar grown as seed compared to the same cultivar grown for consumption. As a result of such variables, the management profile or recommendations for a cultivar may vary within a region because of the purpose of production, and between regions because of differences in environment. One of the requirements for a cultivar to succeed is that the management profile should be available to producers at the time of cultivar release; the grower should not pay the cost of learning the peculiarities of each new cultivar by trial and error. On the other hand, the breeder cannot predict management requirements for regions remote from the location where the cultivar was developed; this becomes the responsibility of the management specialist. It is important, however, for the breeder to provide informa-

tion on the production traits of new cultivars to facilitate the development of management profiles. In North America this responsibility is usually shared by the breeder and the management and extension specialists (McKeown et al. 1990). It can also be undertaken by an independent organization such as the National Institute of Agricultural Botany, which performs this role in the UK (Richardson 1979).

The development of management profiles is the last step in the successful development of a new cultivar. If breeding program objectives have been properly set in keeping with industry requirements, superior cultivars can continue to be produced by achieving new combinations and selections of the many traits described above. While assessment of advanced selections and cultivar description are being completed, the supply of certified seed at the time of introduction can be assured by rapid propagation. Taken together, these are the essential components for successfully breeding potatoes for long-day, temperate climates.

IX. SUMMARY

Advances in potato breeding are being made in many areas: the use of haploids, the recognition of the narrow genetic base of breeding populations and the use of primitive cultivated species, the transfer into cultivars of specific resistance genes from wild species, knowledge of the heritability of an increasing number of quantitative traits, and a better understanding of the effectiveness of selection methods. Since its establishment in 1972 the International Potato Center in Lima, Peru, although focusing on developing country needs, has been a strong, positive influence on all potato research.

These advances are contributing to the release of many new potato cultivars. Nevertheless, the potato industries of North America and Europe continue to be dominated by two old cultivars: 'Russet Burbank' (pre-1890) and 'Bintje' (1910), respectively (Howard 1970). It is fortuitous that these cultivars have been so well suited for the manufacture of frozen french fries that were not commercialized until the 1950s. Nevertheless, there have been significant improvements in cultivars for the french fry and chip markets, for early maturity, and for resistances to diseases and pests. In many countries, especially those with plant breeders' rights, partnerships between private and public sector breeders have ensured a wide choice of available cultivars.

The stage appears set for cultivar improvement to continue. Improvements in understanding the characteristics of good processing quality are making selection for processing less empirical; this should lead to the development of well adapted cultivars with processing qualities better

suited to industry requirements. There are worldwide needs for cultivars that can be produced in sustainable agricultural systems, possibly with less fertilizers, and certainly with less pesticides and sprout inhibitors. A recent international workshop identified major breeding topics requiring international cooperation: true potato seed, diploid genotypes, gene mapping, breeding for resistance to major diseases and pests, and breeding for stress tolerance (Van der Zaag 1987). The germplasm resources to achieve these objectives, and the techniques for screening and evaluation, are available.

There is considerable excitement in some sectors of the potato industry about the possible contributions of biotechnology to potato improvement. The already significant impact of biotechnology is indicated by references in many sections of this review. The first cultivars transformed with virus coat protein genes are being evaluated in field trials in several countries. In the meantime, work continues with synthesized genes, and with the study of the potential of RFLPs. Such techniques will assist in improving existing cultivars, but they will not replace the requirement to evaluate and select new cultivars.

LITERATURE CITED

- Abdalla, M. M. F., and J. G. Th. Hermesen. 1971. A two-locus system of gametophytic incompatibility in *Solanum phureja* and *S. stenotomum*. *Euphytica* 21:345–350.
- Accatino, P., S. J. Peloquin, and M. S. Cipar. 1973. Inheritance of potato chip color at the diploid and tetraploid levels of ploidy. *Am. Potato J.* 50:535.
- Adams, J. B. 1975. Comments on aphid resistance in potatoes. *Am. Potato J.* 52:313–315.
- Adams, S. E., R. A. C. Jones, and R. H. A. Coutts. 1984. Occurrence of resistance-breaking strains of potato virus X in potato stocks in England and Wales. *Plant Pathol.* 33:435–437.
- Adams, S. E., R. A. C. Jones, and R. H. A. Coutts. 1986. Expression of potato virus X resistance gene Rx in potato leaf protoplasts. *J. Gen. Virol.* 67:2341–2345.
- Ainsworth, C. C., and P. J. Sharp. 1989. The potential role of DNA probes in plant variety identification. *Plant Varieties Seeds* 2:27–34.
- Alam, Z. 1972. Inheritance of scab resistance in 24-chromosome potatoes. Ph.D. Thesis, Univ. of Wisconsin, Madison.
- Amirouche, L., T. Stuchbury, and S. Matthews. 1985. Comparisons of cultivar performance on different nutrient media in a routine method for potato micropropagation. *Potato Res.* 28:469–478.
- Amoah, V., and P. Grun. 1988. Cytoplasmic substitution in *Solanum*. I. Seed production, germination, and sterilities of reciprocal backcross generations. *Potato Res.* 31:113–119.
- Amoah, V., P. Grun, and R. R. Hill, Jr. 1988. Cytoplasmic substitution in *Solanum*. II. Tuber characteristics of reciprocal backcross progeny. *Potato Res.* 31:121–127.
- Ancora, G., and A. Sonnino. 1987. In vitro mutation in potato. Chap. IV. 12. 408–424. In: Y. P. S. Bajaj (ed.), *Biotechnology in agriculture and forestry*. Vol. 3: Potato. Springer-Verlag, Berlin.

- Anderson, J. A. D., and H. W. Howard. 1980. Effectiveness of selection in the early stages of potato breeding programmes. *Potato Res.* 24:289-299.
- Andow, D. A., and D. P. Davis. 1989. Agricultural chemicals: food and environment, p. 191-234. In: D. Pimental and C. W. Hall (eds.), *Food and natural resources*. Academic Press Inc., San Diego.
- Anon. 1983. Outline for variety releases. *Am. Potato J.* 60:62-63.
- Arndt, S., and G. Schenk. 1989. Langzeitlagerung virusinfizierten in-vitro Materials der Kartoffel. (Long-term maintenance of virus-infected in vitro potato material.) *Arch. Phytopathol. Pflanzenschutz*, Berlin. 25:295-296.
- Arntzen, F. K., and J. Bakker. 1988. Variation in number of cysts formed on susceptible potato cultivars with various populations of *Globodera rostochiensis* and *G. pallida*. *Euphytica* 5:99-104.
- Arntzen, F. K., and D. Wouters. 1989. Selection for partial resistance to potato cyst nematodes in *Solanum tuberosum* and *S. phureja*, p. 71-75. In: K. M. Louwes, H. A. J. M. Toussaint, and L. M. W. Dellaert (compilers), *Parental line breeding and selection in potato breeding*. Pudoc, Wageningen.
- Austin, S., E. Lojkowska, M. K. Ehlenfeldt, A. Kelman, and J. P. Helgeson. 1988. Fertile interspecific somatic hybrids of *Solanum*: A novel source of resistance to *Erwinia* soft rot. *Phytopathology* 78:1216-1220.
- Australian Plant Quarantine Service. 1983. Plant tissue culture and quarantine. p. 4. Conditions for the import of plant tissue cultures into Australia. Dept. Primary Industry, Canberra, Australia.
- Azad, H. R., J. R. Davis, W. C. Schnathorst, and C. I. Kado. 1987. Influence of verticillium wilt resistant and susceptible potato genotypes on populations of antagonistic rhizosphere and rhizoplane bacteria and free nitrogen fixers. *Appl. Microbiol. Biotechnol.* 26:99-104.
- Baerecke, M. L. 1958. Blattrollresistenzzüchtung (Breeding for leafroll resistance). p. 97-106. In: H. Kappert and W. Rudort (eds.), *Handbuch der Pflanzenzüchtung*. Paul Parey, Berlin.
- Baerecke, M. L. 1967. Überempfindlichkeit gegen das S-virus der Kartoffel in einem bolivianischen Andigena Klon. (Hypersensitivity to potato virus S in a Bolivian Andigena clone.) *Züchter* 37:281-286.
- Bagnall, R. H. 1961. Hypersensitivity to viruses A and X in Canadian and American potato varieties. *Am. Potato J.* 38:192-202.
- Bagnall, R. H. 1977. Resistance to the aphid-borne viruses in the potato, p. 501-526. In: K. F. Harris and K. Maramorosch (eds.), *Aphids as virus vectors*. Academic Press, New York.
- Bagnall, R. H., and G. C. C. Tai. 1986a. Field resistance to potato virus Y in potato assessed by cluster analysis. *Plant Dis.* 70:301-304.
- Bagnall, R. H., and G. C. C. Tai. 1986b. Potato leafroll virus: Evaluation of resistance in potato cultivars. *Plant Dis.* 70:621-623.
- Bagnall, R. H., and D. A. Young. 1972. Resistance to virus S in the potato. *Am. Potato J.* 49:196-201.
- Bain, R. A., and M. C. M. Pérombelon. 1988. Methods of testing potato cultivars for resistance to soft rot of tubers caused by *Erwinia carotovora* subsp. *atroseptica*. *Plant Pathol.* 37:431-437.
- Bajaj, Y. P. S. 1981. Regeneration of plants from potato meristems freeze-preserved for 24 months. *Euphytica*. 30:141-145.
- Bajaj, Y. P. S. 1986. Cryopreservation of potato somaclones, p. 244-250. In: J. Semal (ed.), *Somaclonal variations and crop improvement: Proceedings of a seminar*. Gembloux, Belgium, 3-5 September 1985. *Advances in agricultural biotechnology*. 20. Martinus

- Nijhoff, Boston.
- Bång, H. 1984a. Jämförande studier av olika resistensmetoder för Phoma-röta och Fusarium-röta [Comparative studies of different methods of resistance against gangrene (*Phoma exigua* var. *foveata*) and dry rot (*Fusarium solani* var. *coeruleum*). Växtskyddsrapporter 27:51–67. Swedish Univ. of Agr. Sciences, Uppsala.
- Bång, H. 1984b. Mottaglighet för Phoma-och Fusarium-röta i svenskt sortmaterial. [Susceptibility to gangrene (*Phoma exigua* var. *foveata*) and dry rot (*Fusarium solani* var. *coeruleum*) in potato varieties cultured in Sweden]. Växtskyddsrapporter. 27:1–23. Swedish Univ. of Agr. Sciences, Uppsala.
- Banville, G. J. 1974. The development and the use of an inoculum for field evaluation of the reaction of potatoes to *Rhizoctonia solani* (Kühn). *Am. Potato J.* 51:305 (Abstr.).
- Banville, G. J. 1987. The control of fungal diseases (except late blight), p. 298–308. In: G. Boiteau, R. P. Singh, and R. H. Parry (eds.), *Potato pest management in Canada*. Proc. Symp. Improving Potato Pest Protection, Fredericton, N. B.
- Barker, H. 1987. Multiple components of the resistance of potatoes to potato leafroll virus. *Ann. Appl. Biol.* 111:641–648.
- Barker, H., and B. D. Harrison. 1984. Expression of genes for resistance to potato virus Y—potato plants and protoplasts. *Ann. Appl. Biol.* 105:539–545.
- Beekman, A. G. B. 1987. Breeding for resistance, p. 162–170. In: J. A. de Bokx and J. P. H. Van der Want (eds.), *Viruses of potatoes and seed-potato production*. 2nd ed. Pudoc, Wageningen.
- Beekman, A. G. B., K. M. Louwes, L. M. W. Dellaert, and A. E. F. Neele. 1986. Potato research of tomorrow: Drought tolerance, virus resistance and analytic breeding methods. Proc. Int. Seminar, Wageningen, Oct. 1985. Pudoc, Wageningen.
- Behnke. 1980. Selections of dihaploid potato callus for resistance to the culture filtrate of *Fusarium oxysporum*. *Z. Pflanzenz.* 85:254–258.
- Binding, H., S. M. Jain, J. Finger, G. Mordhorst, R. Nehls, and J. Gressel. 1982. Somatic hybridization of an atrazine resistant biotype of *Solanum nigrum* with *Solanum tuberosum*. Part 1. Clonal variation in morphology and in atrazine sensitivity. *Theor. Appl. Genet.* 63:273–277.
- Birhman, R. K., and M. L. H. Kaul. 1989a. Flower production, male sterility and berry setting in *Andigena* potato. *Theor. Appl. Genet.* 78:884–888.
- Birhman, R. K., and M. L. H. Kaul. 1989b. Variability components and genetic parameters in *Andigena* potato. *Biol. Zent.* 108:209–219.
- Bjor, T. 1987a. Laboratory screening for resistance to gangrene and to fusarium dry rot in potato. *Potato Res.* 30:517–524.
- Bjor, T. 1987b. Testing the resistance of potato genotypes to tuber late blight. *Potato Res.* 30:525–532.
- Bjor, T., and L. Roer. 1980. Testing the resistance of potato varieties to common scab. *Potato Res.* 23:33–47.
- Blomquist, A. W., and F. I. Lauer. 1962. First clonal generation potato progeny performance at two Minnesota locations. *Am. Potato J.* 39:460–462.
- Bogucki, S., and D. C. Nelson. 1980. Length of dormancy and sprouting characteristics of ten potato cultivars. *Am. Potato J.* 57:151–157.
- Böhler, G., F. Escher, and J. Solms. 1986. Evaluation of cooking quality of potatoes using sensory and instrumental methods. 1. Sensory evaluation. *Lebensm.-Wiss. u.-Technol.* 19:338–343.
- Böhler, G., F. Escher, and J. Solms. 1987. Evaluation of cooking quality of potatoes using sensory and instrumental methods. 2. Instrumental evaluation. *Lebensm.-Wiss. u.-Technol.* 20:207–216.
- Bolkan, H. A., and H. T. Wenham. 1973. Pathogenicity of potato sclerotial isolates of

- Rhizoctonia solani* to potato shoots. New Zeal. J. Expt. Agr. 1:383-385.
- Bonierbale, M. W., R. L. Plaisted, and S. D. Tanksley. 1988. RFLP maps based on a common set of clones reveal modes of chromosomal evolution in potato and tomato. *Genetics* 120:1095-1103.
- Booth, C. 1971. The genus *Fusarium*. Commonwealth Agr. Bureau, CMI, Kew, U. K.
- Boulton, R. E., G. J. Jellis, and A. M. Squire. 1987. Breeding for resistance to potato viruses with special reference to cDNA probes, p. 86-87. In: G. J. Jellis and D. E. Richardson (eds.), *The production of new potato varieties: Technological advances*. Cambridge Univ. Press, Cambridge.
- Boulton, R. E., G. J. Jellis, and A. M. Squire. 1988. An improved method of evaluating resistance to potato virus Y and potato leafroll virus in a breeding programme. *Plant Varieties Seeds* 1:109-115.
- Bourne, W. F., D. C. McCalmont, and R. L. Wastie. 1981. Assessing potato tubers for susceptibility to bacterial softrot (*Erwinia carotovora* subsp. *atroseptica*). *Potato Res.* 24:409-415.
- Boyd, A. E. W. 1952a. Dry-rot disease of the potato. IV. Laboratory methods used in assessing variations in tuber susceptibility. *Ann. Appl. Biol.* 39:322-329.
- Boyd, A. E. W. 1952b. Dry-rot disease of the potato. IV. Varietal differences in tuber susceptibility obtained by injection and riddle-abrasion methods. *Ann. Appl. Biol.* 39:339-350.
- Boyd, A. E. W. 1972. Potato storage diseases. *Rev. Plant Pathol.* 51:297-321.
- Boyes, C. J., P. S. Hogan, R. G. Hadley, and D. H. Mitten. 1988. Genetic transformation of potato cultivar 'Norchip' with *Agrobacterium*. *HortScience* 23:754.
- Brodie, B. B. 1984. Nematode parasites of potato, p. 167-212. In: W. R. Nickle (ed.), *Plant and insect nematodes*. Marcel Dekker Inc., New York.
- Brodie, B. B., and W. F. Mai. 1989. Control of golden nematode in the U.S. *Annu. Rev. Phytopathol.* 27:443-461.
- Broertjes, C., and A. M. Van Harten. 1978. Potato, p. 55-69. In: *Application of mutation breeding methods in the improvement of vegetatively propagated crops. Developments in Crop Science* (2). Elsevier Scientific Publishing Co., Amsterdam.
- Brown, C. R. 1985. Genetic studies and breeding of resistance to PLRV, PVY, and PVX, p. 17-44. In: *Present and future strategies for potato breeding and improvement*. Int. Potato Center, Lima, Peru.
- Brown, E., and W. Riley. 1976. Greening of potato tubers: Varietal response to controlled exposure to light. *J. Nat. Inst. Agr. Bot.* 14:70-76.
- Brown, J. 1987. A comparison between single plant plots and five plant plots for the initial selection stage of a potato breeding programme. *Euphytica* 36:711-718.
- Brown, J., and P. D. S. Caligari. 1986. The efficiency of seedling selection for yield and yield components in a potato breeding programme. *Z. Pflanzenzücht.* 96:53-62.
- Brown, J., and P. D. S. Caligari. 1988. The use of multivariate cross prediction methods in the breeding of a clonally reproduced crop (*Solanum tuberosum*). *Heredity* 60:147-153.
- Brown, J., and P. D. S. Caligari. 1989. Cross prediction in a potato breeding programme by evaluation of parental material. *Theor. Appl. Genet.* 77:246-252.
- Brown, J., P. D. S. Caligari, M. F. B. Dale, G. E. L. Swan, and G. R. Mackay. 1988. The use of cross prediction methods in a practical potato breeding programme. *Theor. Appl. Genet.* 76:33-38.
- Brown, J., P. D. S. Caligari, and G. R. Mackay. 1987a. The repeatability of progeny means in the early generations of a potato breeding program. *Ann. Appl. Biol.* 110:365-370.
- Brown, J., P. D. S. Caligari, G. R. Mackay, and G. E. L. Swan. 1984. The efficiency of seedling selection by visual preference in a potato breeding programme. *J. Agr. Sci., Camb.* 103:339-346.

- Brown, J., P. D. S. Caligari, G. R. Mackay, and G. E. L. Swan. 1987b. The efficiency of visual selection in early generations of a potato breeding programme. *Ann. Appl. Biol.* 110:357-363.
- Bryan, J. E. 1988. Implementation of rapid multiplication and tissue culture methods in third world countries. *Am. Potato J.* 65:199-207.
- Buritica, P., and J. Velandia. 1977. Un metodo para seleccionar semilla sexual de papa por resistencia a *Rhizoctonia solani*. *Fitopatol. Colomb.* 6:49-56.
- Burton, W. G. 1989. The potato. Third Ed. Longman Scientific and Technical, Harlow.
- Busch, L. V. 1966. Susceptibility of potato varieties to Ontario isolates of *Verticillium albo-atrum*. *Am. Potato J.* 43:439-442.
- Butkiewicz, H., and M. A. Dziewonska. 1982. Selection of first-year potato seedlings for resistance to potato leafroll virus. *Potato Res.* 25:265-268.
- CIP. 1979. Report of the planning conference on the exploration, taxonomy and maintenance of potato germ plasm. III. October 1979. Int. Potato Center, Lima, Peru.
- CIP. 1984. Potatoes for the developing world. Int. Potato Center, Lima, Peru.
- CIP. 1985. Innovative methods for propagating potatoes. Rpt. XVIII Planning Conf. December 1984. Int. Potato Center, Lima, Peru.
- Caligari, P. D. S., J. Brown, and R. J. Abbott. 1986. Selection for yield and yield components in the early generations of a potato breeding programme. *Theor. Appl. Genet.* 73:218-222.
- Caligari, P. D. S., G. R. Mackay, H. E. Stewart, and R. L. Wastie. 1984. A seedling progeny test for resistance to potato foliage blight (*Phytophthora infestans* (Mont.) de Bary). *Potato Res.* 27:43-50.
- Caligari, P. D. S., G. R. Mackay, H. E. Stewart, and R. L. Wastie. 1985. Confirmatory evidence for the efficacy of a seedling progeny test for resistance to potato foliage blight (*Phytophthora infestans* (Mont.) de Bary). *Potato Res.* 28:439-442.
- Caligari, P. D. S., and A. Nachmias. 1988. Screening for field resistance to early blight (*Alternaria solani*) in potatoes. *Potato Res.* 31:451-460.
- Caligari, P. D. S., and W. Powell. 1989. Variability in response of potato cultivars to micropropagation. *Ann. Appl. Biol.* 115:115-121.
- Caligari, P. D. S., W. Powell, K. Liddell, M. J. DeMaine, and G. E. L. Swan. 1988. Methods and strategies for detecting *Solanum tuberosum* dihaploids in interspecific crosses with *S. phureja*. *Ann. Appl. Biol.* 112:323-328.
- Caligari, P. D. S., and R. L. Wastie. 1985. Assessment of a glasshouse test for measuring the resistance of potato cultivars to common scab. *Potato Res.* 28:379-387.
- Camadro, E. L., and S. J. Peloquin. 1981. Cross-incompatibility between two sympatric polyploid *Solanum* species. *Theor. Appl. Genet.* 60:65-70.
- Camadro, E. L., and S. J. Peloquin. 1982. Selfing rates in two polyploid *Solanums*. *Am. Potato J.* 59:197-204.
- Campbell, C. L., and J. A. Duthie. 1989. Sampling for disease assessment, p. v-ix. In: W. F. Wilcox (ed.), *Biological and cultural tests for control of plant disease*, v. 4. Am. Phytopathol. Soc. Press, St. Paul, MN.
- Cantelo, W. W., L. W. Douglass, L. L. Sanford, S. L. Sinden, and K. L. Deahl. 1987. Measuring resistance to the Colorado potato beetle (Coleoptera: Chrysomelidae) in potato. *J. Entomol. Sci.* 22:245-252.
- Canto Saenz, M., and M. Mayer de Scurrah. 1977. Races of the potato cyst nematode in the Andean region and a new system of classification. *Nematologica* 23:340-349.
- Cappadocia, M., D. S. K. Cheng, and R. Ludlum-Simonette. 1984. Plant regeneration from in vitro culture of anthers of *Solanum chacoense* Bitt. and interspecific diploid hybrids *S. tuberosum* L. $\times$ *S. chacoense* Bitt. *Theor. Appl. Genet.* 69:139-143.
- Cappadocia, M., D. S. K. Cheng, and R. Ludlum-Simonette. 1986. Self-compatibility in doubled haploids and their F1 hybrids, regenerated via anther culture in self-

- incompatible *Solanum chacoense* Bitt. Theor. Appl. Genet. 72:66–69.
- Carnegie, S. F., and A. M. Cameron. 1983. Testing potato cultivars for susceptibility to skin spot (*Polyscytalum pustulans*). Potato Res. 26:69–72.
- Carnegie, S. F., and J. Colhoun. 1983. Effects of plant nutrition on susceptibility of potato leaves to *Phytophthora infestans*. Phytopathol. Z. 108:242–250.
- Carroll, C. P. 1982. A mass-selection method for the acclimatization and improvement of edible diploid potatoes in the United Kingdom. J. Agr. Sci. (Camb.) 99:631–640.
- Carroll, C. P., and M. J. De, Maine. 1989. The agronomic value of tetraploid F1 hybrids between potatoes of Group Tuberosum and Group Phureja/Stenotomum. Potato Res. 32:447–456.
- Cassells, A. C. 1985. Genetic, epigenetic and non-genetic variation in tissue culture derived plants, p. 111–120. In: A. Schäfer-Menuhr (ed.), In vitro techniques. Propagation and long term storage. Martinus Nijhoff/Dr W. Junk, Boston.
- Cassells, A. C., G. Farrell, and E. M. Goetz. 1986. Variation in the tissue culture progeny of the chimera potato (*Solanum tuberosum* L.) variety 'Golden Wonder', p. 202–212. In: J. Semal (ed.), Somaclonal variations and crop improvement: Proceedings of a seminar. Gembloux, Belgium, 3–5 September 1985. Advances in agricultural biotechnology. 20. Martinus Nijhoff, Boston.
- Chand, T., and C. Logan. 1982. Reaction of ten potato cultivars to stem canker and black scurf caused by *Rhizoctonia solani*. Ann. Appl. Biol. v. 100 Suppl. Tests Agrochem. Cultiv. 3:102–103.
- Chandra, R., M. D. Upadhyaya, and K. K. Jha. 1985. Regeneration of plants from rachis tissue of the potato in vitro. J. Indian Potato Assoc. 12:88–91.
- Chase, S. S. 1963. Analytic breeding in *Solanum tuberosum* L.—A scheme utilizing parthenotes and other diploid stocks. Can. J. Genet. Cytol. 5:359–363.
- Chavez, R., C. R. Brown, and M. Iwanaga. 1988a. Transfer of resistance to PLRV titer buildup from *Solanum etuberosum* to a tuber-bearing *Solanum* gene pool. Theor. Appl. Genet. 76:129–135.
- Chavez, R., M. T. Jackson, P. E. Schmiediche, and J. Franco. 1988b. The importance of wild potato species resistant to the potato cyst nematode, *Globodera pallida* Pa4 and Pa5 in potato breeding. I. Resistance studies. Euphytica 37:9–14.
- Chrzanowska, M., and H. Zagórska. 1982. Selekcja rodów ziemniaka odpornych na wirus y na podstawie sztucznego zakażenia roślin w szklarni (Selection of potato clones resistant to PVY on the basis of artificial inoculation in the glasshouse). Biul. Inst. Ziemniaka 28:25–33.
- Chubey, B. B., and G. Mazza. 1983. A non-destructive method for the rapid evaluation of boiling quality of potato tubers. Am. Potato J. 60:693–698.
- Chuquillanqui, C., and R. A. C. Jones. 1980. A rapid technique for assessing the resistance of families of potato seedlings to potato leafroll virus. Potato Res. 23:121–128.
- Cipar, M. S., and C. H. Lawrence. 1972. Scab resistance of haploids from two *Solanum tuberosum* cultivars. Am. Potato J. 49:117–119.
- Cockerham, G. 1970. Genetical studies on resistance to potato viruses X and Y. Heredity 25:309–348.
- Coffin, R. H., R. Y. Yada, K. L. Parkin, B. Grodzinski, and D. W. Staley. 1987. Effect of low temperature storage on sugar concentrations and chip color of certain processing potato cultivars and selections. J. Food Sci. 52:639–645.
- Cole, C. S. 1980. Potato tuber damage—breeder's problems. Ann. Appl. Biol. 96:354–357.
- Colon, L. T., and D. J. Budding. 1988. Resistance to late blight (*Phytophthora infestans*) in ten wild *Solanum* species. Euphytica 5:77–86.
- Conway, W. S. 1989. Altering nutritional factors after harvest to enhance resistance to post-harvest disease. Phytopathology 79:1384–1387.

- Copeland, R., and R. A. Fox. 1987. Potato tuber rot, p. 97–100. In: Potato disease assessment keys. Eur. Assoc. for Potato Res., Section for Pathology.
- Cordeiro, M. T., W. R. Maluf, and J. E. C. Miranda. 1983. Analyses of stability and genotypic similarity in a set of potato (*Solanum tuberosum* L.) cultivars. *Rev. Brasil. Genet.* 1:279–294.
- Correll, D. S. 1962. The potato and its wild relatives. Texas Research Foundation, Renner, Texas.
- Corsini, D., and J. J. Pavék. 1986. Fusarium dry-rot resistant potato germplasm. *Am. Potato J.* 63:629–638.
- Corsini, D. L., J. R. Davis, and J. J. Pavék. 1985. Stability of resistance of potato to strains of *Verticillium dahliae* from different vegetative compatibility groups. *Plant Dis.* 69:980–982.
- Corsini, D. L., J. J. Pavék, and J. R. Davies. 1988. *Verticillium* wilt resistance in non cultivated tuber-bearing *Solanum* species. *Plant Dis.* 72:148–151.
- Coxon, D. T. 1984. Methodology for glycoalkaloid analysis. *Am. Potato J.* 61:169–183.
- Cribb, P. J., and J. G. Hawkes. 1986. Experimental evidence for the origin of *Solanum tuberosum* subspecies *andigena*, p. 383–404. In: W. G. D'Arcy (ed.), *Solanaceae: Biology and systematics*. Columbia Univ. Press, New York.
- Cruikshank, G., H. E. Stewart, and R. L. Wastie. 1982. An illustrated assessment key for foliage blight of potatoes. *Potato Res.* 25:213–214.
- Dale, M. F. B. 1989. Resistance and tolerance of potato cyst nematodes as objectives within a breeding programme, p. 66–70. In: K. M. Louwes, H. A. J. M. Toussaint, and L. M. W. Dellaert (compilers), *Parental line breeding and selection in potato breeding*. Pudoc, Wageningen.
- Dale, M. F. B., M. S. Phillips, R. M. Ayres, M. Hancock, M. Holliday, G. R. Mackay, and S. J. Jones. 1988. The assessment of the tolerance of partially resistant potato clones to damage by the potato cyst nematode *Globodera pallida* at different sites and in different years. *Ann. Appl. Biol.* 113:79–88.
- Dale, P. J., and R. B. Flavell. 1988. Evaluation of genetically engineered plants, p. 73–76. In: R. T. Fraley, N. M. Frey, and J. Schell (eds.), *Genetic improvements of agriculturally important crops: Progress and issues*. *Curr. Commun. Mol. Biol.* Cold Spring Harbor Lab. 1988.
- Dalianis, C. D., R. L. Plaisted, and L. C. Peterson. 1966. Selection for freedom from after cooking darkening in a potato breeding program. *Am. Potato J.* 43:207–215.
- D'Arcy, W. G. 1972. *Solanaceae studies II: Typification of subdivisions of Solanum*. *Ann. Missouri Bot. Gard.* 59:262–278.
- Darso, U. 1987. Long-term results of a tuber slice test for relative resistance to late blight. *Potato Res.* 30:9–22.
- Davidson, T. M. W. 1973. Assessing resistance to leafroll in potato seedlings. *Potato Res.* 16:99–108.
- Davies, A. M. C., and P. J. Blincow. 1984. Glycoalkaloid content of potatoes and potato products sold in the UK. *J. Sci. Food Agr.* 35:553–557.
- Davies, H. T., and N. C. Dixon. 1976. Evaluation of potato texture by taste and by appearance. *Am. Potato J.* 53:205–210.
- Davies, H. T., and G. R. Johnston. 1965. First clonal generation potato seedling selection at two locations. *Am. Potato J.* 42:186–189.
- Davies, H. T., and G. R. Johnston. 1968. Second clonal generation potato seedling selection at two locations. *Am. Potato J.* 45:150–153.
- Davies, H. T., and G. R. Johnston. 1974. Reliability of potato selection in the first clonal generation. *Am. Potato J.* 51:8–11.
- Davies, H. T., H. L. McEwen, and N. C. Dixon. 1975. Field testing potatoes for resistance

- to leafroll and virus Y. *Am. Potato J.* 52:151-155.
- Davila, C., and E. N. Fernandez-Northcote. 1984. Factors affecting mass screening of seedlings for resistance to potato virus Y administered by a spray gun. *Fitopatología* 19:43-44.
- Davis, J. R. 1985. Approaches to control of potato early dying caused by *Verticillium dahliae*. *Am. Potato J.* 62:177-185.
- Davis, J. R., J. J. Pavék, and D. L. Corsini. 1983. A sensitive method for quantifying *Verticillium dahliae* colonization in plant tissue and evaluating resistance among potato genotypes. *Phytopathology* 73:1009-1014.
- Deahl, K. L., M. E. Gallegly, and R. J. Young. 1974. Laboratory testing of potato tubers for multigenic resistance to late blight. *Am. Potato J.* 51:324-329.
- De Block, M. 1988. Genotype-independent leaf disc transformation of potato (*Solanum tuberosum*) using *Agrobacterium tumefaciens*. *Theor. Appl. Genet.* 76:767-774.
- Dědic, P. 1979. Detectability and translocation of potato virus A in potato plants after artificial inoculation. *Potato Res.* 22:357-360.
- De Greef, W., R. Delon, M. De Block, J. Leemans, and J. Botterman. 1989. Evaluation of herbicide resistance in transgenic crops under field conditions. *Bio/Technology* 7:61-64.
- Deimling, S., J. Zitzlsperger, and G. Wenzel. 1988. Somatic fusion for breeding of tetraploid potatoes. *Plant Breed.* 101:181-189.
- De Jong, H. 1981. Inheritance of russetting in cultivated diploid potatoes. *Potato Res.* 24:309-313.
- De Jong, H. 1983. Inheritance of sensitivity to the herbicide metribuzin in cultivated diploid potatoes. *Euphytica* 32:41-48.
- De Jong, H. 1987. Inheritance of pigmented tuber flesh in cultivated diploid potatoes. *Am. Potato J.* 64:337-343.
- De Jong, H., and P. R. Rowe. 1972. Genetic markers in inbred clones of cultivated diploid potatoes. *Potato Res.* 15:200-208.
- De Jong, H., and G. C. C. Tai. 1977. Analysis of tetraploid-diploid hybrids in cultivated potatoes. *Potato Res.* 20:111-121.
- De Jong, H., and T. R. Tarn. 1984. Using germplasm in potato breeding in Canada. *Canada Agr.* 30(3 and 4):12-14.
- Dellaert, L. M. W., and R. Hoekstra. 1987. Resistance to potato cyst nematodes, *Globodera* spp., in wild and primitive *Solanum* species. *Potato Res.* 30:579-587.
- Dellaert, L. M. W., and J. H. Vinke. 1987. Testing potatoes for resistance to *Globodera pallida* pathotype Pa-3; resistance spectra of plant genotypes and virulence spectra of Pa-3 isolates. *Rev. Nematol.* 4:445-453.
- Dellaert, L. M. W., H. Vinke, and K. Meyer. 1988. The inheritance of resistance to the potato cyst nematode *Globodera pallida* Pa-3 in wild *Solanum* species with broad spectrum resistance. *Euphytica* S:105-116.
- De,Maine, M. J. 1978a. Field resistance to late blight and potato root eelworm in Group *Tuberosum* dihaploids. *Euphytica* 27:305-315.
- De,Maine, M. J. 1978b. The inheritance, in diploid potatoes, of yield and of rate of sprout growth during storage. *Potato Res.* 21:163-170.
- De,Maine, M. J. 1982. An evaluation of the use of dihaploids and unreduced gametes in breeding for quantitative resistance to potato pathogens. *J. Agr. Sci. Camb.* 99:79-83.
- De,Maine, M. J. 1988. Testing the tuber deformation resistance of tetraploid and diploid potatoes. *J. Agr. Sci., Camb.* 110:445-449.
- De,Maine, M. J., and P. D. S. Caligari. 1988. Assessments of the resistance of potato cultivars and breeder's clones to external mechanical damage. *J. Agr. Sci., Camb.* 110:527-530.
- De,Maine, L. A. Farrer, and M. S. Phillips. 1986. Breeding for quantitative resistance to

- potato cyst nematode (*Globodera pallida*) in tetraploid potatoes using dihaploids and unreduced gametes. *Euphytica* 35:1001-1006.
- Desborough, S. L. 1985. Potato proteins, p. 329-351. In: P. H. Li (ed.), *Potato physiology*. Academic Press, New York.
- De Vos, N. E., E. J. Pell, R. R. Hill, and R. H. Cole. 1983. Laboratory versus field response of potato genotypes to oxidant stress. *Plant Dis.* 67:173-176.
- Dimock, M. B., and W. M. Tingey. 1985. Resistance in *Solanum* spp. to the Colorado potato beetle. Mechanisms, genetic resources and potential, p. 79-106. In: D. N. Ferro and R. H. Voss, *Proc. Symp. Colorado Potato Beetle. XVIIth Int. Congr. Ent. Res. Bull.* 704. Mass. Agr. Expt. Sta.
- Dionne, L. A. 1958. 2,4-Dichlorophenoxyacetic acid as an aid to seed production when widely separated *Solanum* species are crossed. *Nature* 181:361.
- Dionne, L. A. 1963. Studies on the use of *Solanum acaule* as a bridge between *Solanum tuberosum* and species in the series *Bulbocastana*, *Cardiophylla* and *Pinnatisecta*. *Euphytica* 12:263-269.
- Dodds, J. H. 1988. Tissue culture technology: Practical application of sophisticated methods. *Am. Potato J.* 65:167-180.
- Dodds, K. S. 1962. Classification of cultivated potatoes, p. 517-550. In: D. S. Correll, *The Potato and its wild relatives*. Texas Research Foundation, Renner, Texas.
- Dorozhkin, B. N., N. A. Sakara, A. K. Novoselov, and S. A. Reiter. 1979. Evaluation of the combining ability of potato varieties for yield and its components by the two-tester topcross method. *Sov. Genet.* 15:1359-1363.
- Doster, M. A., J. A. Sweigard, and W. E. Fry. 1989. The influence of host resistance and climate on the initial appearance of foliar late blight of potato from infected seed tubers. *Am. Potato J.* 66:227-233.
- Douches, D. S., K. Ludlam, and W. Linnell. 1989. Use of RFLP's and isoenzymes to fingerprint North American cultivars. *Proc. 1st Intl. Symp. Molec. Biol. Potato*, 13-18 Aug. 1989, Bar Harbour, Maine, USA p. 24. (Abstr.).
- Douches, D. S., and C. F. Quiros. 1987. Use of 4x-2x crosses to determine gene-centromere map distances of isozyme loci in *Solanum* species. *Genome* 29:519-527.
- Douglas, D. R., and J. J. Pavék. 1972. Screening potatoes for field resistance to early blight. *Am. Potato J.* 49:1-6.
- Dourado, A. M., and E. H. Roberts. 1984. Chromosome aberrations induced during storage in barley and pea seeds. *Ann. Bot.* 54:767-779.
- Dowley, L. J. 1972a. Varietal susceptibility of potato tubers to *Rhizoctonia solani* in Ireland. *Ireland J. Agr. Res.* 11:281-285.
- Dowley, L. J. 1972b. Reliability of methods of assessing the degree of tuber attack by common scab of potatoes. *Potato Res.* 15:263-265.
- Dunwell, J. M., and N. Sunderland. 1973. Anther culture of *Solanum tuberosum* L. *Euphytica* 22:317-323.
- Dwelle, R. B., Kleinkopf, G. E., R. K. Steinhorst, and J. J. Pavék. 1979. Measurements of gross photosynthetic rate and leaf area as a potential tool for screening selections from potato breeding programs. *Am. Potato J.* 56:459.
- Dykstra, T. 1956. A new method for screening first-year potato seedlings for scab resistance. *Phytopathology* 46:57-58.
- Dziewonska, M. A. 1986. Development of parental lines for breeding of potatoes resistant to viruses and associated research in Poland, p. 96-100. In: A. G. B. Beekman, K. M. Louwes, L. M. W. Dellaert, and A. E. F. Neele (eds.), *Potato research of tomorrow*. Pudoc, Wageningen.
- EAPR. 1987. Potato disease assessment keys. *Eur. Assoc. for Potato Res. Section for Pathology*.

- Ehlenfeldt, M. K., and R. E. Hanneman, Jr. 1984. The use of endosperm balance number and 2n gametes to transfer exotic germplasm in potato. *Theor. Appl. Genet.* 68:155-161.
- Ehlenfeldt, M. K., and R. E. Hanneman, Jr. 1988. Genetic control of endosperm balance number (EBN): Three additive loci in a threshold-like system. *Theor. Appl. Genet.* 75:825-832.
- Ehlenfeldt, M. K., D. F. Lopez-Portilla, A. A. Boe, and R. H. Johansen. 1990. Reducing sugar accumulation in progeny families of cold chipping potato clones. *Am. Potato J.* 67:83-92.
- Erjefält, L. 1986. Potato breeding: Objectives of the present potato breeding in Sweden, p. 196-203. In: G. Olsson (ed.), *Svalöf 1886-1986: Research and results in plant breeding*. Svalöf, A. B., Svalöv, Sweden.
- Escande, A., and W. Radtke. 1973. Comparación de métodos de inoculación con *Fusarium eumartii* en cultivares de papa (Comparison of inoculation methods with *Fusarium eumartii* in potato cultivars). *Rev. Investig. Agropec. INTA, Bs. As. Argentina, Ser. 5, Patología Vegetal* 10:211-233.
- Espinoza, N. O., and J. H. Dodds. 1985. Adventitious shoot formation on cultured potato roots. *Plant Sci.* 41:121-124.
- Evans, N. E., D. Foulger, L. Farrer, and S. W. J. Bright. 1986. Somaclonal variation in explant-derived potato clones over three tuber generations. *Euphytica* 35:353-361.
- Ewing, E. E., A. H. Senesac, and J. B. Sieczka. 1981. Effects of short periods of chilling and warming on potato sugar content and chipping quality. *Am. Potato J.* 58:633-647.
- Faulkner, J. S. 1982. Breeding herbicide-tolerant crop cultivars by conventional methods, p. 235-256. In: H. M. LeBaron and J. Gressel, *Herbicide resistance in plants*. Wiley, New York.
- Federer, W. T. 1956. Augmented (or Hoonuiaku) designs. *The Hawaiian Planters' Record* 55:191-207.
- Ferro, D. N. 1985. Pest status and control strategies of the Colorado potato beetle, p. 1-8. In: D. N. Ferro and R. H. Voss, 1985. *Proc. Symp. Colorado Potato Beetle, XVIIth Int. Congr. Ent. Res. Bull.* 704. Mass. Agri. Exp. Sta.
- Fischnich, O., and H. Krug. 1959. Gibberellin in der Hand des Kartoffelzüchters (Gibberellin in the hand of the potato breeder). *Der Kartoffelbau* 9:189-191.
- Fish, N., and M. G. K. Jones. 1988. A comparison of tissue culture response between related tetraploid and dihaploid *S. tuberosum* genotypes. *Plant Cell, Tissue & Organ Culture*. 15:201-210.
- Forcella, F. 1987. Herbicide-resistant crops: Yield penalties and weed thresholds for oilseed rape (*Brassica napus* L.). *Weed Res.* 27:31-34.
- Foroughi-Wehr, B., W. Friedt, R. Schuchmann, F. Köler, and G. Wenzel. 1986. In vitro selection for resistance, p. 35-44. In: J. Semal (ed.), *Somaclonal variations and crop improvement*. Advances in Agricultural Biotechnology. Martinus Nijhoff, Dordrecht, Boston.
- Forsund, E. 1987a. Keys applicable for qualitative characters in potato research, p. 6-18. In: *Potato disease assessment keys*. Eur. Assoc. for Potato Res., Section for Pathology.
- Forsund, E. 1987b. Black scurf (*Rhizoctonia solani* Kühn) on tubers, roots, stems and stolons of the potato plants, p. 39-48. In: *Potato disease assessment keys*. Eur. Assoc. for Potato Res., Section for Pathology.
- Forsund, E. 1987c. Potato skin spot (*Polyscytalum pustulans* (Owen and Wakef.) Ellis) on tubers and subsoil parts of the potato plants, p. 87-90. In: *Potato disease assessment keys*. Eur. Assoc. for Potato Res., Section for pathology.
- Foxe, M. J., and J. Prakash. 1986. Expression of resistance to potato virus X in isolated potato protoplasts. *Arch. Virol.* 88:167-174.
- Frandsen, N. O. 1958. Resistenzzüchtung gegen pilzliche und bakterielle Krankheiten der Kartoffel (Breeding for resistance to fungal and bacterial potato diseases), p. 71-97. In:

- H. Kappert and W. Rudolf, *Handbuch der Pflanzenzüchtung*, vol.3. Paul Parey, Berlin.
- Frank, J., S. S. Leach, and R. E. Webb. 1976. Evaluation of potato clone reaction to *Rhizoctonia solani*. *Plant Dis. Rptr.* 60:910-912.
- Frank, J. A., R. E. Webb, and D. R. Douglas. 1979. Evaluation of several USDA potato clones for resistance to early blight. *Plant Dis. Rptr.* 63:392-394.
- Frank, J. A., and D. R. Wilson. 1972. Evaluation of three inoculation methods used to screen potatoes for resistance to *Rhizoctonia solani*. *Plant Dis. Rptr.* 56:348-351.
- French, W. M., and M. J. Bailey. 1980. Potato damage assessment. *Ann. Appl. Biol.* 96:343.
- Frey, K. J., and T. Horner. 1957. Heritability in standard units. *Agron. J.* 49:59-62.
- Friesen, G. H., and D. A. Wall. 1984. Response of potato (*Solanum tuberosum*) cultivars to metribuzin. *Weed Sci.* 32:442-444.
- Fritz, N., and R. E. Hanneman, Jr. 1989. Interspecific incompatibility due to stylar barriers in tuber-bearing and closely related non-tuber-bearing *Solanums*. *Sex. Plant Reprod.* 2:184-192.
- Fry, W. E. 1980. Integration of host resistance and pesticides to manage disease, p. 259-264. In: *Prot. Ecol. v. 2*. Elsevier, Amsterdam.
- Fry, W. E. 1982. *Principles of plant disease management*. Academic Press, New York.
- Fry, W. E., A. E. Apple, and J. A. Bruhn. 1983. Evaluation of potato late blight forecasts modified to incorporate host resistance and fungicide weathering. *Phytopathology* 73:1054-1059.
- Fry, W. E., and B. G. Tweedy. 1983. Introduction to disease control, p. 401-404. In: T. Kommedahl and P. H. Williams (eds.), *Challenging problems in plant health*. Am. Phytopathol. Soc. Press, St. Paul, MN.
- Gans, P. T., W. D. Carson, and M. B. Bishop. 1987. The susceptibility of potato cultivars to powdery scab caused by *Spongospora subterranea* (Wallr.) Lagerh. *J. Nat. Inst. Agr. Bot.* 17:337-343.
- Gans, P. T., and P. Wooster. 1987. Methods for calculating 1-9 values to express the resistance of potato varieties to diseases, p.153-156. In: G. J. Jellis and D. E. Richardson (eds.), *The production of new potato varieties: Technological advances*. Cambridge Univ. Press, Cambridge.
- Garcia, V. S., H. D. Thurston, and A. T. Tschanz. 1977. A greenhouse method for large scale testing of potatoes for general resistance to *Phytophthora infestans*. *Plant Dis. Rptr.* 61:820-822.
- Gardner, M. E., R. Schmidt, and F. J. Stevenson. 1945. The Sequoia potato: A recently-introduced insect resistant variety. *Am. Potato J.* 22:97-103.
- Gaur, P. C., J. Gopal, and M. S. Rana. 1983. Combining ability for yield, its components and tuber dry matter in potato. *Indian J. Agr. Sci.* 53:876-879.
- Gaur, P. C., P. K. Gupta, and H. Kishore. 1978a. Genetic components of tuber yield and quality characters in potato. *J. Indian Potato Assoc.* 5:32-37.
- Gaur, P. C., H. Kishore, and P. K. Gupta. 1978b. Morphological and genetic variability for some quantitative characters in potato. *J. Indian Potato Assoc.* 5:70-75.
- Gawronski, S. W., L. C. Haderlie, R. H. Callihan, and H. Gawronska. 1986. Mechanism of metribuzin tolerance: Herbicide metabolism as a basis for tolerance in potatoes. *Weed Res.* 26:307-314.
- Gebhardt, C., E. Ritter, T. Debener, U. Schachtschabel, B. Walkemeier, H. Uhrig, and F. Salamini. 1989. RFLP analysis and linkage mapping in *Solanum tuberosum*. *Theor. Appl. Genet.* 78:65-75.
- Genet, R. A., and J. A. D. Anderson. 1985. Potato breeding in New Zealand, p. 23-27. In: *Potato growing: A changing scene*. Spec. Publ., Agron. Soc. New Zealand.
- Gibson, R. W., M. G. K. Jones, and N. Fish. 1988. Resistance to potato leafroll virus and

- potato virus Y in somatic hybrids between dihaploid *Solanum tuberosum* and *S. brevidens*. Theor. Appl. Genet. 76:113-117.
- Gibson, R. W., and R. T. Plumb. 1977. Breeding plants for resistance to aphid infestation, p. 473-500. In: K. F. Harris, and K. Maramorosch (eds.), *Aphids as vectors*. Academic Press, New York.
- Gilliland, T. J. 1989. Electrophoresis of sexually and vegetatively propagated cultivars of allogamous species. *Plant Varieties Seeds* 2:15-25.
- Glendinning, D. R. 1976. Neo-Tuberosum: New potato breeding material. 4. The breeding system of Neo-Tuberosum, and the structure and composition of the Neo-Tuberosum gene-pool. *Potato Res.* 19:27-36.
- Glendinning, D. R. 1979. Enriching the potato gene pool using primitive cultivars. *Proc. Conf. Broadening Genet. Base Crops*, Wageningen, 1978. Pudoc, Wageningen, p. 39-45.
- Glendinning, D. R. 1983. Potato introductions and breeding up to the early 20th century. *New Phytol.* 94:479-505.
- Glendinning, D. R., and M. S. Phillips. 1988. Resistance to potato cyst nematodes *Globodera rostochiensis* and *G. pallida* in the British Neo-Tuberosum potato population. *Potato Res.* 31:477-483.
- Gmelig Meyling, H. D., and K. B. Bodlaender. 1981. Varietal differences in growth, development and tuber production of potatoes. *Neth. J. Agr. Sci.* 29:113-127.
- Goodman, R. M. 1987. Future potential, problems, and practicalities of herbicide-tolerant crops from genetic engineering. *Weed Sci.* 35(Suppl.):28-31.
- Goth, R. W., and R. E. Webb. 1985. Resistance to potato virus S in *Solanum tuberosum*. *Phytopathology* 75:625. (Abstr.).
- Götz, J. 1980. Probleme der Resistenzprüfung von Kartoffeln gegenüber der Fusarium-Trockenfäule (Problems of testing potatoes for resistance to *Fusarium dry rot*). *Arch. Phytopathol. Pflanzensch.* 16:251-258.
- Gould, W. A., and S. Plimpton. 1985. Quality evaluation of potato cultivars for processing. North Central Regional Res. Publ. 305. Ohio Agricultural Research and Development Center, Ohio Univ. Wooster, Ohio. p. 1-25.
- Grasmick, M. E. and S. A. Slack. 1985. Effect of potato spindle tuber viroid on sexual reproduction and viroid transmission in true potato seed. *Can. J. Bot.* 64:336-340.
- Gray, D., and J. C. Hughes. 1982. Tuber quality, p. 504-544. In: P. M. Harris (ed.), *The potato crop: The scientific basis for improvement*. Chapman and Hall, London.
- Gregory, P., W. M. Tingey, D. A. Ave, and P. Y. Bouthyette. 1986. Potato glandular trichomes: A physicochemical defense mechanism against insects. *Am. Chem. Soc. Symp. Series* 296:160-167.
- Gressel, J., N. Cohen, and H. Binding. 1984. Somatic hybridization of an atrazine resistant biotype of *Solanum nigrum* with *Solanum tuberosum*. *Theor. Appl. Genet.* 67:131-134.
- Griess, H. 1981. Nachbarwirkung auf den Ertrag in Kartoffelsortenprüfungen (Border effects on yields in potato variety trials). *Arch. Acker- und Pflanzenbau und Bodenkunde* 25:711-716.
- Groden, E., and R. A. Casagrande. 1986. Population dynamics of the Colorado potato beetle, *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae), on *Solanum berthaultii*. *J. Econ. Entomol.* 79:91-97.
- Grun, P. 1979. Evolution of the cultivated potato: A cytoplasmic analysis, p. 655-666. In: J. G. Hawkes, R. N. Lester, and A. D. Skelding (eds.), *The biology and taxonomy of the Solanaceae*. Linn. Soc. Symp. Ser. No. 7. Academic Press, London.
- Gubb, I. R., J. C. Hughes, M. T. Jackson, and J. A. Callow. 1989. The lack of enzymic browning in the wild potato species *Solanum hjertingii* compared with commercial *Solanum tuberosum* varieties. *Ann. Appl. Biol.* 114:579-586.
- Gunenc, Y., and R. W. Gibson. 1980. Effects of glandular foliar hairs on the spread of potato

- virus Y. *Potato Res.* 23:345-351.
- Gunn, R. E., G. J. Jellis and N. C. Starling. 1985. Improved resistance to common scab (*Streptomyces scabies*) in protoplast derived potato somaclones previously selected for high yield. *Ann. Appl. Biol.* v. 102 Suppl., Tests Agrichem. Cultiv. 6:162-163.
- Gunn, R. E., G. J. Jellis, P. J. Webb, and N. C. Starling. 1983. Comparison of three methods for assessing varietal differences in resistance to common scab disease (*Streptomyces scabies*) of potato. *Potato Res.* 26:175-178.
- Haeder, H. E., and H. Beringer. 1983. Potato. Symposium on potential productivity of field crops under different environments. Potential productivity of field crops under different environments. Los Baños, Philippines. p. 307-317.
- Hampson, M. C., and K. G. Proudfoot. 1974. Potato wart disease, its introduction to North America, distribution and control problems in Newfoundland. *FAO Plant Protection Bull.* 22:53-64.
- Hanneman, R. E., Jr. 1979. Thoughts on the adaptation of wild species of the potato to the north temperate region, p. 1-4. In: Rept. to the NCR-84 Potato Genetics Techn. Comm. U.S.D.A. and Univ. of Wisconsin, Madison.
- Hanneman, R. E., Jr. 1989. The potato germplasm resource. *Am. Potato J.* 66:655-667.
- Hanneman, R. E., Jr., and J. B. Bamberg. 1986. Inventory of tuber-bearing *Solanum* species. Univ. of Wisconsin, Madison. Bull. 533.
- Hansen, L. M. 1985. Testing potato clones for resistance to *Globodera rostochiensis* (Ro₁) and *Globodera pallida* (Pa₂ and Pa₃) by root-ball screening. *Eur. Plant Prot. Org. Bull.* 15:193-198.
- Harrewijn, P. 1986. Vector resistance of potato to aphids with respect to potato leafroll virus, p. 85-95. In: A. G. B. Beekman, K. M. Louwes, L. M. W. Dellaert, and A. E. F. Neele (eds.), *Potato research for tomorrow*. Pudoc, Wageningen.
- Harrison, B. D., and J. I. Cooper. 1974. Studies on the nature of the resistance of potato cultivar to tobacco rattle virus. *Potato Res.* 17:348 (Abstr.).
- Harrison, M. D. 1978a. Potato early blight: Importance and control, p. 93-109. In: Rpt. Planning Conf. Control Important Fungal Dis. Potatoes. Int. Potato Center, Lima, Peru.
- Harrison, M. D. 1978b. The *Rhizoctonia* disease of potatoes: Importance and control, p. 129-150. In: Rept. Planning Conf. Control Important Fungal Dis. Potatoes. Int. Potato Center, Lima, Peru.
- Hawkes, J. G. 1979. Evolution and polyploidy in potato species, p. 637-646. In: J. G. Hawkes, R. N. Lester, and A. D. Skelding (eds). *The biology and taxonomy of the Solanaceae*. Linnean Soc. Symp. Series. No. 7. Academic Press, London.
- Hawkes, J. G. 1982. Biosystematics of the potato, p. 15-69. In: P. M. Harris (ed.), *The potato crop: The scientific basis for improvement*. Chapman and Hall, London.
- Hawkes, J. G. 1990. *The potato: Evolution, biodiversity and genetic resources*. Belhaven Press, London.
- Hawkes, J. G., and J. P. Hjerting. 1969. The potatoes of Argentina, Brazil, Paraguay and Uruguay—A biosystematic study. *Ann. of Bot. Mem.* 3. Oxford University Press, Oxford.
- Hawkes, J. G., and J. P. Hjerting. 1989. *The potatoes of Bolivia—Their breeding value and evolutionary relationships*. Clarendon Press, Oxford.
- Haynes, F. L. 1980. Progress and future plans for the use of Phureja-Stenotomum populations, p. 80-88. In: Rept. Planning Conf. 1980. Utilization of the genetic resources of the potato III. Int. Potato Center, Lima, Peru.
- Haynes, K. G., and F. L. Haynes. 1988. The effect of day and night temperatures on bud initiation and flowering in diploid potatoes. *Am. Potato J.* 65:589-596.
- Haynes, K. G., F. L. Haynes, and W. R. Henderson. 1989. Heritability of specific gravity of diploid potato under high temperature growing conditions. *Crop Sci.* 29:622-625.

- Heagle, A. S. 1989. Ozone and crop yield. *Annu. Rev. Phytopathol.* 27:397-423.
- Helgeson, J. P. 1989a. Somatic hybridization of wild *Solanum* species with potato: A potential source of diversity for breeders, p. 87-94. In: K. M. Louwes, H. A. J. M. Toussaint, and L. M. W. Dellaert (compilers), Parental line breeding and selection in potato breeding. Proc. joint Conf. EAPR-EUCARPIA, Wageningen, Dec. 1988. Pudoc, Wageningen.
- Helgeson, J. P. 1989b. Postharvest resistance through breeding and biotechnology. *Phytopathology* 79:1375-1377.
- Hellenas, K.-E. 1986. A simplified procedure for quantification of potato glycoalkaloids in tuber extracts by H.p.l.c.; comparison with ELISA and a colorimetric method. *J. Sci. Food Agr.* 37:776-782.
- Henshaw, G. G., P. D. Keefe, and J. F. O'Hara. 1985. Cryopreservation of potato meristems, p. 155-160. In: A. Schäfer-Menuhr (ed.), *In vitro techniques. Propagation and long term storage*. Martinus Nijhoff/Dr. W. Junk, Boston.
- Hermesen, J. G. Th. 1974. Utilization of non-cultivated wild species, p. 27-32. In: Strategy for utilization. Rept. Planning Conf. Utilization of Genetic Resources, Int. Potato Center, Lima, Peru.
- Hermesen, J. G. Th. 1980. Breeding for apomixis in potato: Pursuing a utopian scheme. *Euphytica* 29:595-607.
- Hermesen, J. G. Th. 1983. Utilization of wide crosses in potato breeding, p. 115-131. In: Present and future strategies for potato breeding and improvement. Rpt. 26th Planning Conf. Int. Potato Center, Lima, Peru.
- Hermesen, J. G. Th. 1989. Current use of potato collections, p. 68-87. In: A. H. D. Brown, O. H. Frankel, D. R. Marshall, and J. T. Williams (eds.), *The use of plant genetic resources*. Cambridge Univ. Press., Cambridge.
- Hermesen, J. G. Th., E. Jongedijk, and M. S. Ramanna. 1987. An evaluation of new methods and techniques for potato breeding. Proc. 10th Trien. Conf. Eur. Assoc. Potato Res. (EAPR), p. 30-42.
- Hermesen, J. G. Th., and E. Sawicka. 1979. Incompatibility and incongruity in tuber-bearing *Solanum* species, p. 445-453. In: J. G. Hawkes, R. N. Lester, and A. D. Skelding (eds.), *The biology and taxonomy of the Solanaceae*. Linn. Soc. Symp., No. 7. Academic Press, London.
- Hermesen, J. G. Th., J. Sonneveld, D. Vreugdenhil, D. Van Ballegooijen, and E. Staas-Ebregt. 1978. Genetics of self-compatibility in dihaploids of *Solanum tuberosum* L. 5. The S-genotype of tetraploid potato cultivar Gineke. *Euphytica* 27:385-388.
- Hermesen, J. G. Th., and J. Verdenius. 1973. Selection from *Solanum tuberosum* Group Phureja of genotypes combining high-frequency haploid induction with homozygosity for embryo-spot. *Euphytica* 22:244-259.
- Hermundstad, S. A., and S. J. Peloquin. 1985. Germplasm enhancement with potato haploids. *J. Hered.* 76:463-467.
- Hermundstad, S., and S. J. Peloquin. 1986. Tuber yield and tuber traits of haploid-wild species F_1 hybrids. *Potato Res.* 29:289-297.
- Hermundstad, S. A., and S. J. Peloquin. 1987. Breeding at the 2x level and sexual polyploidization, p. 197-210. In: G. J. Jellis and D. E. Richardson (eds.), *The production of new potato varieties: Technological advances*. Cambridge Univ. Press, Cambridge.
- Herriott, A. B., F. L. Haynes, Jr., and P. B. Shoemaker. 1986. The heritability of resistance to early blight in diploid potatoes (*Solanum tuberosum*, subsp. *phureja* and *stenotomum*). *Am. Potato J.* 63:229-232.
- Herriott, A. B., F. L. Haynes Jr., and P. B. Shoemaker. 1990. Inheritance of resistance to early blight disease in tetraploid $\times$ diploid crosses of potatoes. *HortScience* 25:224-226.
- Hilali, A., F. I. Lauer, and R. E. Veilleux. 1988. Effect of environment and direction of

- hybridization on genetic variability in two diploid potato populations. *Potato Res.* 31:247-256.
- Hoekema, A., M. J. Huisman, L. Molendijk, P. J. M. Van den Elzen, and B. J. C. Cornelissen. 1989. The genetic engineering of two commercial potato cultivars for resistance to potato virus X. *Bio/Technology* 7:273-278.
- Hoekstra, R. 1989. The effects of silverthiosulphate and gibberellic acid on flowering and seed set of potato, p. 202. In: K. M. Louwes, H. A. J. M. Toussaint, and L. M. W. Dellaert (compilers), *Parental line breeding and selection in potato breeding*. Proc. joint Conf. EAPR-EUCARPIA, Wageningen, Dec. 1988. Pudoc, Wageningen.
- Hoekstra, R., and L. Seidewitz. 1987. Evaluation data on tuber-bearing *Solanum* species. Institut für Pflanzenbau und Pflanzenzüchtung der FAL—Stichting voor Plantenveredeling (SVP).
- Holden, J. H. W. 1981. The contribution of breeding to the improvement of potato quality, p. 37-52. In: EAPR Survey Papers. 8th trien. conf. European Association for Potato Research. München, 1981.
- Hooker, W. J. (ed.), 1981. *Compendium of potato diseases*. Am. Phytopath. Soc. Press, St. Paul, MN.
- Hoopes, R. W., and R. L. Plaisted. 1987. Potato, p. 385-436. In: W. R. Fehr (ed.), *Principles of cultivar development*. Vol. 2. Crop species. pp. 385-436. Macmillan, New York.
- Hoopes, R. W., R. L. Plaisted, and A. G. Cubillos. 1980. Yield and fertility of reciprocal cross *Tuberosum*—*Andigena* hybrids. *Am. Potato J.* 57:275-284.
- Hosaka, K. 1986. Who is the mother of the potato? Restriction endonuclease analysis of chloroplast DNA of cultivated potatoes. *Theor. Appl. Genet.* 72:606-618.
- Hosaka, K., and R. E. Hanneman, Jr. 1988. Origin of chloroplast DNA diversity in the Andean potatoes. *Theor. Appl. Genet.* 76:333-340.
- Hosaka, K., Y. Ogiwara, M. Matsubayashi, and K. Tsunewaki. 1984. Phylogenetic relationship between the tuberous *Solanum* species as revealed by restriction endonuclease analysis of chloroplast DNA. *Japan. J. Genet.* 59:349-369.
- Hossain, M., and C. Logan. 1983. A comparison of inoculation methods for determining potato cultivar reaction to black leg. *Ann. Appl. Biol.* 103:63-70.
- Hougas, R. W., and S. J. Peloquin. 1958. The potential of potato haploids in breeding and genetic research. *Am. Potato J.* 35:701-707.
- Howard, H. W. 1960. *Potato cytology and genetics*. 1952-1959. *Bibliogr. Genet.* 19:87-216.
- Howard, H. W. 1963. Some potato breeding problems. *Ann. Rep.* 1961-62. Camb. Univ., Plant Breed. Institute. p. 5-12.
- Howard, H. W. 1970. *Genetics of the potato, Solanum tuberosum*. Springer-Verlag, New York.
- Howard, H. W. 1974. Factors influencing the quality of ware potatoes. I. The genotype. *Potato Res.* 17:490-511.
- Howard, H. W. 1982. The production of new varieties, p. 607-646. In: P. M. Harris (ed.), *The potato crop: The scientific basis for improvement*. Chapman and Hall, New York.
- Howard, H. W., R. Johnson, G. E. Russell, and M. S. Wolfe. 1969. Problems in breeding for resistance to diseases and pests, p. 6-36. In: *Annu. Rpt. Plant Breed. Inst.*, Cambridge.
- Howard, H. W., F. A. Langton, and G. J. Jellis. 1976. Testing for field susceptibility of potato tubers to blight (*Phytophthora infestans*) *Plant Pathol.* 25:13-14.
- Hoyman, W. G. 1974. Reaction of *Solanum tuberosum* and *Solanum* species to *Meloidogyne hapla*. *Am. Potato J.* 74:281-286.
- Hsiao, T. H. 1985. Ecophysiological and genetic aspects of geographic variations of the Colorado potato beetle, p. 63-77. In: D. N. Ferro and R. H. Voss, *Proc. Symp. Colorado Potato Beetle*, XVIIth Int. Congr. Ent. Res. Bull. 704. Mass. Agr. Expt. Sta.
- Huamán, Z. 1987. Inventory of Andean potato cultivars with resistance to some pests and

- diseases and other desirable traits. Int. Potato Center, Lima Peru.
- Huamán, Z., and R. W. Ross. 1985. Updated listing of potato species names, abbreviations and taxonomic status. *Am. Potato J.* 62:629-641.
- Huamán, Z., B. Tivoli, and L. de Lindo. 1989. Screening for resistance to *Fusarium* dry rot in progenies of cultivars of *S. tuberosum* ssp. *andigena* with resistance to *Erwinia chrysanthemi*. *Am. Potato J.* 66:357-364.
- Huamán, Z., J. T. Williams, W. Salhuana, and L. Vincent. 1977. Descriptors for the cultivated potato and for the maintenance and distribution of germ plasm collection. Int. Board for Plant Genetic Resources. Rome, Italy.
- Huang, J.-S. 1985. Mechanisms of resistance to root-knot nematodes, p. 165-174. In: J. N. Sasser and C. C. Carter (eds.), *An advanced treatise on Meloidogyne*. Vol. 1, Biology and control. North Carolina State Univ. Graphics.
- Hung, K. S., and N. J. Whitney. 1982. Reaction of two potato cultivars to leaf infection by *Verticillium albo-atrum*. *Can. J. Bot.* 60:554-556.
- Hunnius, W. 1981. Die Qualitätsmerkmale der Kartoffel für die Zukunft (Potato quality characteristics for the future.) p. 7-28. In: *EAPR Survey Papers*. 8th Trien. Conf. European Association for Potato Research. München.
- Irikura, Y. 1975. Induction of haploid plants by anther culture in tuber-bearing species and interspecific hybrids of *Solanum*. *Potato Res.* 18:133-140.
- Iritani, W. M., L. D. Weller, and N. R. Knowles. 1984. Factors influencing incidence of internal brown spot in Russet Burbank potatoes. *Am. Potato J.* 61:335-343.
- Iwama, K., K. Nakaseko, K. Gotoh, and Y. Nishibe. 1979. Varietal differences in root system development and tuber yield. *Japan J. Crop Sci.* 48:403-408.
- Iwama, K., K. Nakaseko, A. Isoda, K. Gotoh, and Y. Nishibe. 1981. Relations between root system and tuber yield in the hybrid population of the potato plants. *Japan J. Crop Sci.* 50:233-238.
- Iwama, K., and S. Nishibe. 1989. Comparison of root characters among cultivated potatoes (*Solanum tuberosum*) and their wild relatives. *Japan J. Crop Sci.* 58:126-132.
- Iwanaga, M., P. Jatala, R. Ortiz, and E. Guevara. 1989. Use of FDR 2n pollen to transfer resistance to root-knot nematodes into cultivated 4x potatoes. *J. Am. Soc. Hort. Sci.* 114:1008-1013.
- Jackson, M. T., J. G. Hawkes, B. S. Male-Kayiwa, and N. W. M. Wanyera. 1988. The importance of the Bolivian wild potato species in breeding for *Globodera pallida* resistance. *Plant Breed.* 101:261-268.
- Jacobsen, E., and W. J. Feenstra. 1989. The use of amylose-free mutant 86.040 in potato breeding, p.123-127. In: K. M. Louwes, H. A. J. M. Toussaint, and L. M. W. Dallaert (compilers), *Parental line breeding and selection in potato breeding*. Proc. joint Conf. EAPR-EUCARPIA, Wageningen, Dec. 1988. Pudoc, Wageningen.
- Jacobsen, T. L., and S. H. Jansky. 1989. Effects of pre-breeding wild species on tuberization of *Solanum tuberosum* haploid-wild species hybrids. *Am. Potato J.* 66:803-811.
- Jakubiec, J., and M. Suska. 1984. Poszukiwanie źródeł odporności na choroby przechowalnice poza *Solanum tuberosum* [Search of sources of resistance to storage diseases outside *Solanum tuberosum*]. *Zesz. Probl. Postępow. Nauk Rolniczych*. 273:95-107.
- James, W. C. 1971. A manual of assessment keys for plant diseases. Canada Agr. Publ. 1458.
- Jatala, P. 1983. An efficient method for screening large numbers of potato seedlings for resistance to *Meloidogyne* species, p. 105-106. In: W. J. Hooker (ed.), *Research for the potato in the year 2000*. Int. Potato Center, Lima, Peru.
- Jayasinghe, U., C. Chuquillanqui, and L. E. Salazar. 1989. Modified expression of virus resistance in potato in mixed virus infections. *Am. Potato J.* 66:137-144.
- Jellis, G. J. 1975. Screening potato clones for resistance to dry rot (*Fusarium solani* var.

- coeruleum). *Ann. Appl. Biol.* 81:417-418.
- Jellis, G. J. 1978. Determining the susceptibility of potato clones to gangrene (*Phoma exigua* var. *foveata*). *Potato Res.* 21:135-143.
- Jellis, G. 1982. Laboratory assessments of the susceptibility of potato tubers to gangrene (*Phoma exigua* var. *foveata*). *Plant Pathol.* 31:171-177.
- Jellis, G. J., R. E. Boulton, N. C. Starling, and A. M. Squire. 1987a. Screening for resistance to diseases in a potato breeding programme, p. 84-85. In: G. J. Jellis and D. E. Richardson (eds.), *The production of new potato varieties: Technological advances*. Cambridge Univ. Press., Cambridge.
- Jellis, G. J., C. N. D. Lacey, R. E. Boulton, S. B. Currell, A. M. Squire, and N. C. Starling. 1986. Early generation screening of potato clones for disease and pest resistance. *Aspects Appl. Biol.* 13:301-305.
- Jellis, G. J., P. S. Phul, and N. C. Starling. 1987b. Evaluation of potato germplasm for resistance to powdery scab (*Spongospora subterranea*). *Ann. Appl. Biol.* v. 110 Suppl., Tests Agrochem. Cultiv. 8:154-155.
- Jellis, G. J., and D. E. Richardson (eds.), 1987. *The production of new potato varieties: Technological advances*. Cambridge Univ. Press, Cambridge.
- Jellis, G. J., and N. C. Starling. 1983. Resistance to powdery dry rot (*Fusarium sulphureum*) in potato tubers. *Potato Res.* 26:295-301.
- Jervis, L., A. L. Shepherd, and M. J. De, Maine. 1986. Variations in soluble tuber proteins in tetraploid, dihaploid and doubled dihaploid potato (*Solanum tuberosum*). *Biochem. Soc. Trans.* 14:1096-1097.
- Johansen, D. G., K. W. Knutson, S. R. Slack, and E. D. Jones. 1984. Recommendations for standards and guidelines for acceptance of tissue cultured potato seed stocks into certification programs. *Am. Potato J.* 61:368-370.
- Johansen, R. H. 1986. New releases and developments in potato varieties for processing. *Proc. National Chipping Potato Sem.* Boston. p. 1-9.
- Johns, T., and S. L. Keen. 1986. Taste evaluation of potato glycoalkaloids by the Aymara: A case study in human chemical ecology. *Human Ecology* 14:437-452.
- Johnson, R. 1987. The challenge of disease resistance, p. 311-323. In: P. R. Day and G. J. Jellis (eds.), *Genetics and plant pathogenesis*. Blackwell Scientific Publications, Oxford.
- Johnston, G. R., and R. G. Rowberry. 1981. Yukon Gold: A new yellow-fleshed, medium-early, high quality table and French-fry cultivar. *Am. Potato J.* 58:241-244.
- Johnston, S. A., T. P. M. den Nijs, S. J. Peloquin, and R. E. Hanneman, Jr. 1980. The significance of genic balance to endosperm development in interspecific crosses. *Theor. Appl. Genet.* 57:5-9.
- Johnston, S. A., and R. E. Hanneman, Jr. 1982. Manipulations of endosperm balance number overcome crossing barriers between diploid *Solanum* species. *Science* 217:446-448.
- Jones, F. G. W., D. M. Parrott, and J. N. Perry. 1981. The gene-for-gene relationship and its significance for potato cyst nematodes and their solanaceous hosts, p. 23-36. In: B. M. Zuckerman, and R. A. Rohde (eds.), *Plant parasitic nematodes*, Vol. III, Academic Press, New York.
- Jones, M. G. K. 1987. Use of protoplast fusion and somaclonal variation in potato breeding, p. 315-326. In: G. J. Jellis, and D. E. Richardson (eds.), *The production of new potato varieties: Technological advances*. Cambridge Univ. Press, Cambridge.
- Jones, R. A. C. 1984. Andean potato viruses and virus strains, and potato quarantine, p. 11-17. In: K. G. Singh (ed.), *Exotic quarantine pests and procedures for introduction of plant materials*. Asian Plant Quarantine Center and Training Institute. Serdang, Malaysia.
- Jones, R. A. C. 1985. Further studies on resistance-breaking strains of potato virus X. *Plant Pathol.* 34:182-189.

- Jongedijk, E. 1985. The pattern of megasporogenesis and megagametogenesis in diploid *Solanum* species hybrids; its relevance to the origin of 2n-eggs and the induction of apomixis. *Euphytica* 34:599-611.
- Jongedijk, E., and M. S. Ramanna. 1988. Synaptic mutants in potato, *Solanum tuberosum* L. I. Expression and identity of genes for desynapsis. *Genome* 30:664-670.
- Jongedijk, E., J. M. A. S. A. Van der Wolk, and L. C. J. M. Suurs. 1990. Analysis of glutamate oxaloacetate transaminase (GOT) isozyme variants in diploid tuberous *Solanum*; inheritance and linkage relationships to *ds1* (desynapsis), *y* (tuber flesh colour), *cr* (crumpled) and *yc* (yellow cotyledon). *Euphytica* 45:155-167.
- Josephson, D. B., and R. C. Lindsay. 1987. c4-Heptenal: An influential volatile compound in boiled potato flavor. *J. Food Sci.* 52:328-331.
- Karp, A., R. S. Nelson, E. Thomas, and S. W. J. Bright. 1982. Chromosome variation in protoplast-derived potato plants. *Theor. Appl. Genet.* 63:265-272.
- Kaul, M. L. H. 1988. Male sterility in higher plants. Springer-Verlag, New York.
- Kawchuk, L. M., R. R. Martin, and J. McPherson. 1989. Transgenic plants containing the potato leafroll virus coat protein gene. *Proc. First Int. Symp. Molec. Biol. Potato*. Aug. 13-18, 1989. Bar Harbour, ME. (Abstr.), p. 52.
- Keller, E. R., and M. Baumgartner. 1982. Beeinflussung von Qualitätseigenschaften durch Genotyp und Umwelt (The influence of genotype and environment on quality characteristics). *Kartoffelbau* 33:12-15.
- Kelman, A., R. G. McGuire, and K. C. Tzeng. 1989. Reducing the severity of bacterial soft rot by increasing the concentration of calcium in potato tubers, p. 102-123. In: A. W. Engelhard (ed.), *Soilborne plant pathogens: Management of diseases with macro- and microelements*. Am. Phytopathol. Soc. Press, St. Paul, MN.
- Kennedy, G. G. 1976. Host plant resistance and the spread of plant virus. *Environ. Entomol.* 5:827-832.
- Killick, R. J. 1977. Genetic analysis of several traits in potatoes by means of a diallel cross. *Ann. Appl. Biol.* 86:279-289.
- Killick, R. J., and J. F. Malcolmson. 1973. Inheritance in potatoes of field resistance to late blight [*Phytophthora infestans* (Mont.) de Bary]. *Physiol. Plant Pathol.* 3:121-131.
- Killick, R. J., and N. W. Simmonds. 1974. Specific gravity of potato tubers as a character showing small genotype-environment interactions. *Heredity* 32:109-112.
- Kimpinski, J., and T. H. A. Olthof. 1987. Control of nematodes, p. 133-145. In: G. Boiteau, R. P. Singh, and R. H. Parry (eds). *Potato pest management in Canada*. *Proc. Symp. Improving Potato Pest Protection*, Fredericton, N. B.
- Kirkham, R. P. 1986. Screening for resistance to powdery scab disease of potatoes. *Austral. J. Expt. Agr.* 26:245-247.
- Kishore, H., and G. H. Rieman. 1969. A recessive type of immunity to virus X in the potato. *Genetics* 62:171-180.
- Kliffen, C. 1974. A simple biochemical test for the determination of the degree of 'field resistance' of potato leaves to *Phytophthora infestans*. *Potato Res.* 17:354 (Abstr.).
- Kort, J., H. Ross, H. J. Rumpfenhorst, and A. R. Stone. 1977. An international scheme for identifying and classifying pathotypes of potato cyst-nematodes *Globodera rostochiensis* and *G. pallida*. *Nematologica* 23:333-339.
- Krantz, F. A., and C. J. Eide. 1941. Inheritance of reaction to common scab in the potato. *J. Agr. Res.* 63:219-231.
- Krikun, J., and D. Orion. 1979. Verticillium wilt of potato: Importance and control. *Phytoparasitica* 7:107-116.
- Krug, H., G. Wriedt, and W. E. Weber. 1974a. Untersuchungen zur Frühselektion in der Kartoffelzüchtung. I. Untersuchungen an der Sämlingsgeneration (Investigations on early selection in potato breeding. I. Investigation of the seedling generation.)

- Z. Pflanzenzücht. 73:141-162.
- Krug, H., G. Wriedt, and W. E. Weber. 1974b. Untersuchungen zur Frühselektion in der Kartoffelzüchtung. II. Merkmalsbeziehungen zwischen den Generationen und innerhalb der Klongenerationen (Investigations on early selection in potato breeding. II. Character correlations between the generations and within the clonal generations). Z. Pflanzenzücht. 73:163-193.
- Kuc, J. 1984. Steroid glycoalkaloids and related compounds as potato quality factors. Am. Potato J. 61:123-139.
- Kwiatkowski, S., M. W. Martin, C. Brown, and C. J. Sluis. 1988. Serial microtuber formation as a long-term conservation method for *in vitro* potato germplasm. Am. Potato J. 65:369-375.
- Kyte, L. 1987. Plants from test tubes. An introduction to micropropagation. Timber Press, Portland, Oregon.
- Lacey, C. N. D., C. J. Jellis, S. B. Currell, and N. C. Starling. 1987. An early generation screen for combined cyst nematode (*Globodera* spp.) and blight (*Phytophthora infestans*) resistance in potato. Potato Res. 30:59-69.
- Lakshman, D. K., B. D. Bandy, and S. M. Tavantzis. 1990. Evaluation of transgenic plants engineered with an antisense mutated cDNA of potato spindle tuber viroid (PSTV). Am. Potato J. 67:559 (Abstr.).
- Lam, S.-L. 1974. Origin and formation of unreduced gametes in the potato. J. Hered. 65:175-178.
- Lam, S.-L. 1975. Shoot formation in potato tuber discs in tissue culture. Am. Potato J. 52:103-106.
- Lange, W. 1976. Strategy of maintenance and utilization of genetic resources, p. 64-84. In: Rept. planning conf. exploration and maintenance of germ plasm resources. March 1976. Int. Potato Center, Lima, Peru.
- Langerfeld, E. 1984a. Naszfäule und Schwarzbeinigkeit der Kartoffel aus der Sicht jüngerer Forschungsergebnisse. Eine Literaturübersicht (Soft rot and blackleg of potatoes in the light of recent research. A literature survey). Nachrichtenbl. Deut. Pflanzenschutzd. 36:97-103.
- Langerfeld, E. 1984b. *Synchytrium endobioticum* (Schilb.) Perc. Zusammenfassende Darstellung des Erregers des Kartoffelkrebses an hand von Literaturberichten (*Synchytrium endobioticum* (Schilb.) Perc. A comprehensive literature survey of the causal agent of potato wart). Mitteilungen aus der Biologischen Bundesanstalt für Land- und Forstwirtschaft. Berlin-Dahlem, Paul Parey, Berlin.
- Langerfeld, E. 1987a. Methoden bei der Prüfung der Reaktion von Kartoffelsorten gegen Lagerfäuleerreger der Gattung *Fusarium*, p. 101-110. In : Potato disease assessment keys. Eur. Assoc. for Potato Res.. Section for Pathology.
- Langerfeld, E. 1987b. Methoden zur Prüfung der Reaktion von Kartoffelsorten gegen den Erreger des Kartoffelkrebses (*Synchytrium endobioticum*), p. 112-124. In: Potato disease assessment keys. Eur. Assoc. for Potato Res.. Section for Pathology.
- Langton, F. A. 1971. The development of a laboratory method test of assessing potato varietal susceptibility to gangrene caused by *Phoma exigua* var. *foveata*. Potato Res. 14:29-38.
- Langton, F. A. 1972a. The development of a laboratory method of assessing varietal resistance of potato tubers to late blight (*Phytophthora infestans*). Potato Res. 15:290-301.
- Langton, F. A. 1972b. Screening potato clones for resistance to common scab (*Streptomyces scabies*) in the field. J. Agr. Sci. (Camb.) 79:75-81.
- Langton, F. A., and H. Ross. 1982. The effects of colchicine doubling of potato dihaploid × wild species hybrids on eelworm resistance and pollen "stainability". Potato Res. 25:257-263.

- Lapointe, S. L., W. M. Tingey, and T. Zitter. 1987. Potato virus Y transmission reduced in an aphid-resistant potato species. *Phytopathology* 77:819-822.
- Lapwood, D. H. 1978. Important storage pathogens and their control, p. 151-164. In: Rpt. Planning Conf. Control Important Fungal Dis. Potatoes. Int. Potato Center, Lima, Peru.
- Lapwood, D. H., and P. T. Gans. 1984. A method for assessing the field susceptibility of potato cultivars to blackleg (*Erwinia carotovora* subsp. *atroseptica*). *Ann. Appl. Biol.* 104:315-320.
- Lapwood, D. H., and P. J. Read. 1985. A simplified slice method for assessing tuber susceptibility of potato cultivars to *Erwinia carotovora* subsp. *atroseptica*. *Plant Pathol.* 34:284-286.
- Lapwood, D. H., and P. J. Read. 1986. A comparison of methods of seed tuber inoculation for assessing the susceptibility of potato cultivars to blackleg (*Erwinia carotovora* subsp. *atroseptica*) in the field. *Ann. Appl. Biol.* 109:287-297.
- Lapwood, D. H., P. J. Read, and P. T. Gans. 1985. The field susceptibility of potato varieties to blackleg caused by *Erwinia carotovora* subsp. *atroseptica*. *J. Nat. Inst. Agr. Bot.* 17:107-116.
- Lapwood, D. H., P. J. Read, and J. Spokes. 1984. Methods for assessing the susceptibility of potato tubers of different cultivars to rotting by *Erwinia carotovora* subspecies *atroseptica* and *carotovora*. *Plant Pathol.* 33:13-20.
- Lauer, F., J. C. Miller, Jr., N. Andersen, E. Bantari, A. Kallio, S. Munson, P. Orr, D. Preston, D. G. Smallwood, J. Sowokinos, G. Titrud, R. Wenkel, J. Wiersma, and D. Wildung. 1988. Krantz: A russet cultivar for the irrigated sands. *Am. Potato J.* 65:387-391.
- Lauer, F. L., and C. J. Eide. 1963. Evaluation of parent clones of potato for resistance to common scab by the "highest scab" method. *Eur. Potato J.* 6:35-44.
- Lauer, F., and R. Shaw. 1970. A possible genetic source for chipping potatoes from 40°F storage. *Am. Potato J.* 47:275-278.
- Lawrence, C. H., and W. G. Barker. 1963. A study of tuberization in the potato, *Solanum tuberosum*. *Am. Potato J.* 40:349-356.
- Lawrence, T., J. Toll, and D. H. Van Sloten. 1986. Directory of germplasm collections. 2. Root and tuber crops. Int. Board of Plant Gene Resources. Rome.
- Lawson, C., W. Kaniewski, L. Haley, R. Rozman, C. Newell, and N. Turner. 1989. Genetically engineered virus resistance in 'Russet Burbank' potato to potato virus X and potato virus Y, p. 55. *Proc. 1st Int. Symp. Molec. Biol. Potato*, 13-18 Aug., 1989, Bar Harbour, ME. (Abstr.)
- Leach, S. S., B. Bandy, and C. W. Murdoch. 1983. The evaluation of a new method to identify potato clones resistant to *Rhizoctonia solani* Kühn. *Phytopathology* 73:369. (Abstr.)
- Leach, S. S., and R. E. Webb. 1981. Resistance of selected potato cultivars and clones to fusarium dry rot. *Phytopathology* 71:623-629.
- LeBaron, H. M., and J. Gressel (eds.), 1983. *Herbicide resistance in plants*. Wiley, New York.
- Leon, R. D. 1987. The reliability of small plot yield trial data in the estimation of farm scale yields of potatoes. PhD Thesis, Cornell University, Ithaca, NY.
- Levy, D., and N. Kedar. 1985. *Solanum tuberosum*, p. 363-366. In: A. H. Halevy (ed.), *CRC Handbook of flowering*, vol. 4. CRC Press, Inc., Boca Raton, FL.
- Lin, C. S., and G. Pouschinsky. 1983. A modified augmented design for an early stage of plant selection involving a large number of test lines without replication. *Biometrics* 39:553-561.
- Little, G., R. Marquinez, and L. R. Cooke. 1988. The response of twelve potato cultivars to

- infection with *Rhizoctonia solani*. Ann. Appl. Biol. v. 112 Suppl., Tests Agrochem. Cult. 9:88-89.
- Lizarraga, R., Z. Huamán, and J. H. Dodds. 1989. In vitro conservation of potato germplasm at the International Potato Center. Am. Potato J. 66:253-269.
- Logan, C. 1985. Problems associated with testing cultivar susceptibility to blackleg and soft rot, p. 77-78. In: D. C. Graham and M. D. Harrison (eds.), Rept. Int. Conf. Potato Blackleg Disease. Potato Marketing Board and Potato Assoc. of Am.
- Loiselle, F. 1989. Evaluation of chip color and influence of genetic divergence on potato (*Solanum tuberosum* L.) progenies. Ph. D. Thesis. Univ. of Guelph. Guelph, Ontario.
- Loiselle, F., G. C. C. Tai, T. R. Tarn, and B. R. Christie. 1989a. The use of multivariate analyses to eliminate redundant variables when evaluating potatoes for chip quality. Plant Breed. 103:153-162.
- Loiselle, F., G. C. C. Tai, B. R. Christie, and T. R. Tarn. 1989b. Relationship between inbreeding coefficient and clonal selection in a potato cultivar development program. Am. Potato J. 66:747-753.
- Loria, R., and B. A. Kemper. 1986. Relative resistance of potato tubers produced from stem cuttings and seed-piece—propagated plants to *Streptomyces scabies*. Plant Dis. 70:1146-1148.
- Louwes, K. M., and A. E. F. Neele. 1987. Selection for chip quality and specific gravity of potato clones: Possibilities for early generation selection. Potato Res. 30:241-252.
- Louwes, K. M., H. A. J. M. Toussaint, and L. M. W. Dellaert (compilers). 1989. Parental line breeding and selection in potato breeding. Proc. joint Conf. EAPR-EUCARPIA, Wageningen, Dec. 1988. Pudoc, Wageningen.
- Louwing, A., R. Suk, and B. Ros. 1986. Generation of lightsprouts suitable for potato variety identification by means of artificial light. Taxonomy of cultivated plants. Acta Hort. 182.
- Lozoya-Saldaña, H., and I. Miranda-Velázquez. 1987. Growth regulators, photoperiod and flowering in potatoes. Am. Potato J. 64:377-382.
- Luckett, J. D. (ed.). 1961. Symposium on mutation and plant breeding. Cornell Univ., Ithaca, Nov. 28-Dec. 2, 1960. Publ. 891. National Academy of Sciences National Research Council, Washington.
- Lugt, C. 1961. Results of the assessment of the cooking quality of internationally exchanged potato samples. Proc. 1st trienn. Conf. Eur. Assoc. for Potato Res., 12-17 Sept, 1960. Braunschweig. p. 321-323. Wageningen.
- Lynch, D. R., and G. C. Kozub. 1988. An analysis of the response of nine potato genotypes to five prairie environments. Can. J. Plant Sci. 68:1219-1228.
- Lynch, D. R., G. B. Schaalje, G. C. C. Tai, and D. A. Young. 1987. Use of canonical discriminant analysis in assessing the merit of crosses in terms of breeding goals. Am. Potato J. 64:385-396.
- Lynch, D. R., and G. C. C. Tai. 1989. Yield and yield component response of eight potato genotypes to water stress. Crop Sci. 29:1207-1211.
- Lynch, D. R., G. C. C. Tai, D. A. Young, and G. B. Schaalje. 1983. Effect of selecting potato seedlings under maritime conditions on the performance of the first clonal generation under prairie conditions. Am. Potato J. 60:607-615.
- Lyon, G. D. 1989. The biochemical basis of resistance of potatoes to soft rot *Erwinia* spp.—A review. Plant Pathol. 38:313-339.
- Macarthur, A. W., and R. J. Killick. 1976. Environmental and genetic variation in some economically important traits in potatoes. J. Agr. Sci., Camb. 87:39-43.
- Mackay, G. R. 1982. Breeding for resistance to pests and diseases. Scottish Crop Research Institute, Bull. 1, p. 27-34.
- Mackay, G. R. 1987. Selecting and breeding for better potato cultivars, p. 181-196. In:

- A. J. Abbott and R. K. Atkin (eds.), Improving vegetatively propagated crops. Academic Press, San Diego, CA.
- MacKenzie, D. R., W. R. Mills, and J. O. Watts. 1976. Predicting yield and processing quality of potato breeding selections. *Am. Potato J.* 53:87-98.
- Madamba, C. P. 1978. Identification of resistance and tolerance to the root-knot nematode and their practical implications, p. 117-126. In: Developments in the control of nematode pests of potato. Rept. 2nd Nematode Planning Conf. Int. Potato Center, Lima, Peru.
- Madry, W., and L. Ubysz-Borucka. 1983. The investigation of combining ability of potato based on the success fraction of progeny in incomplete diallel crosses. *Potato Res.* 26:247-259.
- Magnus, H. A. 1987. Testing potatoes for resistance to wart (*Synchytrium endobioticum*) in Norway, p. 125-126. In: Potato disease assessment keys. Eur. Assoc. for Potato Res., Section for Pathology.
- Mai, W. F., B. B. Brodie, M. B. Harrison, and P. J. Jatala. 1981. Nematodes, p. 93-101. In: W. J. Hooker (ed.), Compendium of potato diseases. Am. Phytopathol. Soc. Press, St. Paul, MN.
- Malagamba, P., and A. Monares. 1988. True potato seed: Past and present uses. Int. Potato Center, Lima, Peru.
- Malcolmson, J. F. 1976. Assessment of field resistance to blight (*Phytophthora infestans*) in potatoes. *Trans. Brit. Mycol. Soc.* 67:321-360.
- Malcolmson, J. F., and R. J. Killick. 1980. The breeding values of potato parents for field resistance to late blight measured by whole seedlings. *Euphytica* 29:489-495.
- Manzer, F. E., R. V. Akeley, and D. Merriam. 1964. Resistance to powdery scab in *Solanum tuberosum*. *Am. Potato J.* 41:374-376.
- Manzer, F. E., and A. R. McKenzie. 1988. Cultivar response to bacterial ring rot infection in Maine. *Am. Potato J.* 65:333-339.
- Marais, L., and R. Vorster. 1988. Evaluation in pot and field trials of resistance of potato cultivars and breeding lines to common scab caused by *Streptomyces scabies*. *Potato Res.* 31:401-404.
- Maramorosch, K. 1980. Insects and plant pathogens, p. 137-155. In: F. G. Maxwell and P. R. Jennings (eds.), Breeding plants resistant to insects. Wiley, New York.
- Maris, B. 1962. Analyse van aardappelpopulaties ten dienste van de veredeling (Analysis of potato populations as an aid in breeding). Doctoral Dissertation, Agr. Univ., Pudoc, Wageningen.
- Maris, B. 1966. The modifiability of characters important in potato breeding. *Euphytica* 15:18-31.
- Maris, B. 1969. Studies on maturity, yield, under water weight and some other characters of potato progenies. *Euphytica* 18:297-319.
- Maris, B. 1988. Correlations within and between characters between and within generations as a measure for the early generation selection in potato breeding. *Euphytica* 37:205-224.
- Maris, B. 1989. Analysis of an incomplete diallel cross among three ssp. *tuberosum* varieties and seven long-day adapted ssp. *andigena* clones of the potato (*Solanum tuberosum* L.). *Euphytica* 41:163-182.
- Maris, B. 1990. Comparison of diploid and tetraploid potato families derived from *Solanum phureja* × dihaploid *S. tuberosum* hybrids and their vegetatively doubled counterparts. *Euphytica* 46:15-33.
- Maryanski, J. H. 1988. Genetically modified agricultural crops: an FDA perspective, p. 91-94. In: R. T. Fraley, N. M. Frey, and J. Schell (eds.), Genetic improvements of agriculturally important crops: Progress and issues. Curr. Commun. Mol. Biol. Cold Spring

- Harbor Lab. 1988.
- Masson, J., C. Bellini, D. Lancelin, M. Lecerf, P. Guerchie, and G. Pelletier. 1989. Introduction of selectable markers by direct gene transfer and its potential application for somatic hybridization in potato (*Solanum tuberosum* L.), p. 107–110. In: K. M. Louwes, H. A. J. M. Toussaint, and L. M. W. Dellaert (compilers). Parental line breeding and selection in potato breeding. Proc. joint Conf. EAPR—EUCARPIA, Wageningen, Dec. 1988. Pudoc, Wageningen.
- Mastenbroek, C. 1988. Plant breeders' rights, an equitable legal system for new plant cultivars. Expt. Agr. 24:15–30.
- Matern, U., and G. A. Strobel. 1987. IV.5. In vitro production of potatoes bearing resistance to fungal diseases, p. 298–317. In: Y. P. S. Bajaj (ed.), Biotechnology in agriculture and forestry. v.3. Springer-Verlag, Berlin.
- Mathys, G., and E. A. Baker. 1980. An appraisal of the effectiveness of quarantines. Annu. Rev. Phytopathol. 18:85–101.
- Matthews, S., T. Stuchbury, and W. J. Thomson. 1986. The application of micropropagation to seed potato production in Northern Scotland, p. 197–203. In: L. A. Withers and P. G. Alderson (eds.), Plant tissue culture and its applications. Butterworths, London.
- Mayer de Scurrah, M., R. L. Plaisted, and M. L. Harrison. 1973. Resistance to the potato nematode *Heterodera rostochiensis* Woll. in clones derived from *Solanum vernei*. Am. Potato J. 50:9–18.
- Mayer de Scurrah, M., and A. Van der Wal. 1988. Breeding for resistance to potato cyst nematode at CIP, p. 77–89. In: Developments in the control of nematode pests of potato. Rept. 2nd Nematode Planning Conf. Int. Potato Center, Lima, Peru.
- Mazza, G. 1983. A comparison of methods of analysis for sugars in potato tubers. Can. Inst. Food Sci. Technol. J. 16:234–236.
- McComber, D. R., R. A. Lohnes, and E. M. Osman. 1987. Double direct shear test for potato texture. J. Food Sci. 52:1302–1304.
- McKeown, A. W., R. H. Coffin, R. Y. Yada, and S. Squire. 1990. The concept and development of management profiles for potato cultivars and selections. Am. Potato J. 67:527–535.
- McMorran, J. P., and T. C. Allen. 1983. Maintenance, symptoms and distribution of potato viruses X, S, Y, A, M and leafroll in potato tissue culture plantlets. Am. Potato J. 60:839–847.
- McPherson, S., F. Perlak, R. Fuchs, S. MacIntosh, D. Dean, and D. Fischhoff. 1989. Expression and analysis of the insect control protein from *Bacillus thuringiensis* var. *tenebrionis*. Proc. 1st Intl. Symp. Mol. Biol. Potato, 13–18 Aug. 1989, Bar Harbour, Maine, U.S.A. p. 51. (Abstr.)
- Mehlenbacher, S. A., R. L. Plaisted, and W. M. Tingey. 1983. Inheritance of glandular trichomes in crosses with *Solanum berthaultii*. Am. Potato J. 60:699–708.
- Mehlenbacher, S. A., R. L. Plaisted, and W. M. Tingey. 1984. Heritability of trichome density and droplet size in interspecific potato hybrids and relationship to aphid resistance. Crop Sci. 24:320–322.
- Mellor, F. C., and R. Stace-Smith. 1987. Virus-free potatoes through meristem culture, p. 30–39. In: Y. P. S. Bajaj (ed.), Biotechnology in agriculture and forestry. Vol. 3. Potato. Springer-Verlag, New York.
- Mendiburu, A. O., and S. J. Peloquin. 1977a. Bilateral sexual polyploidization in potatoes. Euphytica 26:573–584.
- Mendiburu, A. O., and S. J. Peloquin. 1977b. The significance of 2n gametes in potato breeding. Theor. Appl. Genet. 49:53–61.
- Mendiburu, A. O., and S. J. Peloquin. 1979. Gene-centromere mapping by 4x—2x matings in potatoes. Theor. Appl. Genet. 54:177–180.

- Mendoza, H. A. 1983. Breeding of potato populations at the international potato center. *Int. Potato Center Circ.* 11(3):1-6
- Mendoza, H. A. 1989. Population breeding as a tool for germplasm enhancement. *Am. Potato J.* 66:639-653.
- Mendoza, H. A., and F. L. Haynes. 1974. Genetic relationship among potato cultivars grown in the United States. *HortScience* 9:328-330.
- Menzel, C. M. 1985a. The control of storage organ formation in potato and other species: A review. Part 1. *Field Crop Abstr.* 38:527-537.
- Menzel, C. M. 1985b. The control of storage organ formation in potato and other species: A review. Part 2. *Field Crop Abstr.* 38:581-606.
- Meulemans, M., D. Duchene, and G. Fouarge. 1987. Selection of variants by dual culture of potato and *Phytophthora infestans*, p. 318-331. In: Y. P. S. Bajaj (ed.), *Biotechnology in agriculture and forestry*. v.3. Potato. Springer-Verlag, Berlin.
- Miller-Jones, D. N., and P. J. Howell. 1986. Micropropagation as an aid in quarantine procedures for potato material, p. 257-260. In: L. A. Withers and P. G. Alderson. (eds.), *Plant tissue culture and its agricultural applications*. Butterworths, London.
- Mix, G. 1985. Preservation of old potato varieties, p. 149-153. In: A. Schäfer-Menuhr (ed.), *In vitro techniques. Propagation and long term storage*. Martinus Nijhoff/Dr. W. Junk, Boston.
- Mndolwa, D., G. Bishop, D. Corsini, and J. Pavék. 1984. Resistance of potato clones to the green peach aphid and potato leafroll virus. *Am. Potato J.* 61:713-722.
- Mok, D. W. S., and S. J. Peloquin. 1975. The inheritance of three mechanisms of diplandroid (2n pollen) formation in diploid potatoes. *Heredity* 35:295-302.
- Mondy, N. I., S. Chandra, and W. D. Evans. 1985. Enzymic discoloration and phenolic content of potato tubers from cultivars resistant and susceptible to the golden nematode. *Am. Potato J.* 62:207-213.
- Moorby, J. 1982. The physiology of growth and tuber yield, p. 153-194. In: P. M. Harris (ed.), *The potato crop*. Chapman & Hall, London.
- Moreira, A., R. A. C. Jones, and C. E. Fribourg. 1980. Properties of a resistance-breaking strain of potato virus X. *Ann. Appl. Biol.* 95:93-103.
- Morgan, M. R. A., and D. T. Coxon. 1987. Tolerances: Glycoalkaloids in potatoes, p. 221-230. In: D. H. Watson (ed.) *Natural toxicants in food: Progress and prospects*. Ellis Norwood.
- Morgan, M. R. A., D. T. Coxon, S. Bramham, H. W.-S. Chan, W. M. J. Van Gelder, and M. J. Allison. 1985. Determination of the glycoalkaloid content of potato tubers by three methods including enzyme-linked immunosorbent assay. *J. Sci. Food Agr.* 36:282-288.
- Mountier, N. S. 1985. Techniques for the design of potato cultivar trials, p. 29-31. In: G. D. Hill (ed.), *Potato growing: A changing scene*. Agronomy Soc. of New Zeal., Lincoln.
- Mugnieri, D. 1983. A method for screening potatoes for resistance to *Globodera* spp. under laboratory conditions, p. 137-138. In: W. J. Hooker (ed.), *Research for the potato in the year 2000*. Int. Potato Center, Lima, Peru.
- Mullin, R., and Lauer, F. I. 1966. Breeding behavior of F_1 and inbred potato clones. *Proc. Am. Soc. Hort. Sci.* 89:449-455.
- Muneta, P., and F. Kaisaki. 1985. Ascorbic acid-ferrous iron (Fe^{++}) complexes and after cooking darkening of potatoes. *Am. Potato J.* 62:531-536.
- Munzert, M., and W. Hunnius. 1980. Beziehungen zwischen den Resistenzen gegen Schwarzbeinigkeit, Nasz- und Trockenfäule der Kartoffel (*Solanum tuberosum* L.) (Relation between the resistance to *Erwinia carotovora* and to *Fusarium* spp. in potato). *Z. Pflanzenzücht.* 85:59-70.
- Murakami, N. 1983. Studies on variation and selection of potatoes (*Solanum tuberosum*). *Japan. J. Breed.* 33:160-170.

- Murphy, E. F., R. H. True., and J. H. Hogan. 1967. Detection threshold of sensory panels for mealiness of baked potatoes as related to specific gravity differences. *Am. Potato J.* 44:442-451.
- NIAB. 1985. Disease assessment manual of crop variety trials. National Institute of Agricultural Botany, Cambridge.
- Nachmias, A., and J. Krikun. 1987. Assessment of *Verticillium* wilt (*Verticillium albo-atrum* R. & B. and *V. dahliae* Kleb.) in potato, p. 49-55. In: Potato disease assessment keys. Eur. Assoc. Potato Res., Section for pathology.
- Nachmias, A., M. Tal, and J. Krikun. 1983. Screening for *Verticillium* tolerance by the use of toxic metabolites produced by the pathogen, p. 138. In: W. J. Hooker (ed.), Research for the potato in the year 2000. Int. Potato Center, Lima, Peru.
- Neal, J. J., J. C. Steffens, and W. M. Tingey. 1989. Glandular trichomes of *Solanum berthaultii* and resistance to the Colorado potato beetle. *Entomol. Expt. Appl.* 51:133-140.
- Neele, A. E. F. 1989. Inheritance of some crop physiological components of potato tuber yield, p. 61-65. In: K. M. Louwes, H. A. J. M. Toussaint, and L. M. W. Dellaert (compilers), Parental line breeding and selection in potato breeding. Proc. joint Conf. EAPR-EUCARPIA, Wageningen, Dec. 1988. Pudoc, Wageningen.
- Neele, A. E. F., J. H. M. Barten, and K. M. Louwes. 1988. Effects of plot size and selection intensity on efficiency of selection in the first clonal generation of potato. *Euphytica* 5:27-35.
- Nelson, D. C., and J. R. Sowokinos. 1983. Yield and relationships among tuber size, sucrose and chip color in six potato cultivars on various harvest dates. *Am. Potato J.* 60:949-958.
- Nelson, R. R. 1978. Genetics of horizontal resistance to plant diseases. *Annu. Rev. Phytopathology* 16:359-378.
- Ochoa, C. M. 1962. Los *Solanum* tuberiferos silvestres del Peru (Secc. Tuberarium, subsecc. Hyperbasarthrum). Lima, Peru.
- O'Hair, S. K., C. M. Baker, and H. H. Bryan. 1987. Fluid drilling of embryos in potato improvement—A future possibility, p. 487-498. In: Y. P. S. Bajaj (ed.), Biotechnology in agriculture and forestry. Vol. 3. Potato. Springer-Verlag, New York.
- Okada, K. A., and A. M. Clausen. 1984. Collecting potatoes in Northwest Argentina, 1983. *Am. Potato J.* 64:301-305.
- Oliver, J. L., and J. M. Martínez-Zapater. 1984. Allozyme variability and phylogenetic relationships in the cultivated potato (*Solanum tuberosum*) and related species. *Plant. Syst. Evol.* 148:1-18.
- Oliver, J. L., and J. M. Martínez-Zapater. 1985. A genetic classification of potato cultivars based on allozyme patterns. *Theor. Appl. Genet.* 69:305-311.
- Olsson, K. 1986. The influence of genotype on the effects of impact damage on the accumulation of glycoalkaloids in potato tubers. *Potato Res.* 29:1-12.
- Olsson, K. 1989. Impact damage, gangrene and dry rot in potato. Important biochemical factors in screening for resistance and quality in breeding material. Ph. D. Thesis, Swedish Univ. Agr. Sciences. Svalöf, Stockholm.
- Ooms, G., M. M. Burrell, A. Karp, M. Bevan, and J. Hille. 1987. Genetic transformation in two potato cultivars with T-DNA from disarmed *Agrobacterium*. *Theor. Appl. Genet.* 73:744-750.
- Ormrod, D. P., B. Young, and B. Marie. 1987. Sensitivity of crop plants to gaseous pollution stress. *CRC Critical Rev. Agr.* 1:225-272.
- Ortiz, R., M. Iwanaga, and H. A. Mendoza. 1988. Combining ability and parental effects in 4x-2x crosses for potato breeding. *Potato Res.* 31:643-650.
- Osman, S. F. 1983. Glycoalkaloids in potatoes. *Food Chem.* 11:235-247.
- Osman, S. F., and S. L. Sinden. 1989. High performance liquid chromatographic analysis

- of *Solanum* steroidal alkaloids. *J. Chromatogr.* 479:189–193.
- Otazu, V., and G. A. Secor. 1980. Clinitest: A simple technique for estimation of reducing sugar content of potatoes. *Am. Potato J.* 57:15–20.
- Owens, R. A., and T. O. Diener. 1981. Sensitive and rapid diagnosis of potato spindle tuber viroid by nucleic acid spot hybridization. *Science* 213:670–671.
- Oxtoby, E., and M. A. Hughes. 1989. Breeding for herbicide resistance using molecular and cellular techniques. *Euphytica* 40:173–180.
- Pandey, K. K. 1962a. Incompatibility in some *Solanum* crosses. *Genetica* 33:24–30.
- Pandey, K. K. 1962b. Interspecific incompatibility in *Solanum* species. *Am. J. Bot.* 49:874–882.
- Pandita, M. L., and A. S. Sidhu. 1981. Studies on variability and heritability of some important characters in potato. *Punjab Hort. J.* 21:116–121.
- Parfitt, D. E., and S. J. Peloquin. 1981. The genetic basis for tuber greening in 24-chromosome potatoes. *Am. Potato J.* 58:299–304.
- Parlevliet, J. E. 1979. Components of resistance that reduce the rate of epidemic development. *Annu. Rev. Phytopathol.* 17:203–222.
- Parlevliet, J. E. 1983. Can horizontal resistance be recognized in the presence of vertical resistance in plants exposed to a mixture of pathogen races? *Phytopathology* 73:379.
- Parnell, A., V. S. Bhuva, and E. J. B. Bintcliffe. 1984. The glycoalkaloid content of potato varieties. *J. Nat. Inst. Agr. Bot.* 16:535–541.
- Pavek, J. J. 1987. Some interesting aspects of recent and expected developments in potato breeding in North America (Canada and the United States of America), p. 61–65. In: Hesen, J. C., C. D. Van Loon, J. G. Hermsen, and L. J. Turkensteen (eds.), *Recent and future developments of the potato in the world. Workshop, April 1987, Wageningen. Acta Hort.* 213.
- Pavek, J., D. Corsini, and F. Nissley. 1985. A rapid method for determining blackspot susceptibility of potato clones. *Am. Potato J.* 62:511–517.
- Pelletier, J. R., and W. E. Fry. 1989. Characterization of resistance to early blight in three potato cultivars: Incubation period, lesion expansion rate, and spore production. *Phytopathology* 79:511–517.
- Peloquin, S. J. 1982. Meiotic mutants in potato breeding. *Stadler symp.* 14:99–109. Univ. of Missouri, Columbia.
- Peloquin, S. J. 1983. Genetic engineering with meiotic mutants, p. 311–316. In: D. L. Mulcahy and E. Ottaviano (eds.), *Pollen: Biology and implications for plant breeding.* Elsevier Science Publ. Co., New York.
- Peloquin, S. J., R. W. Hougas, and A. C. Gabert. 1966. Haploidy as a new approach to the cytogenetics and breeding of *Solanum tuberosum*, p. 21–28. In: R. Riley and K. R. Lewis (eds.), *Chromosome manipulation and plant genetics.* Oliver and Boyd, Edinburgh.
- Peloquin, S. J., and M. Iwanaga. 1981. Restorer genes for genetic-cytoplasmic male sterility in cultivated potatoes. *Am. Potato J.* 58:513–514 (Abstr.)
- Peloquin, S. J., S. H. Jansky, and G. L. Yerk. 1989. Potato cytogenetics and germplasm utilization. *Am. Potato J.* 66:629–638.
- Pemajayantha, V., and A. L. Gunasekara. 1982. A study on the optimum plot size for potato experiments. *Tropical Agriculturist.* 138:45–57.
- Pennypacker, B. W. 1989. The rate of mineral nutrition in the control of *Verticillium* wilt, p. 33–45. In: A. W. Engelhard (ed.), *Soilborne plant pathogens: Management of diseases with macro and micro-elements.* Am. Phytopathol. Soc. Press, St. Paul, MN.
- Pérombelon, M. C. M., and A. Kelman. 1980. Ecology of the soft rot *Erwinias*. *Annu. Rev. Phytopath.* 18:361–387.
- Pérombelon, M. C. M., and A. Kelman. 1987. Blackleg and other potato diseases caused by soft rot *Erwinias*: Proposal for revision of terminology. *Plant Dis.* 71:283–285.

- Peters, D. 1986. Mechanisms of virus transmission in relation to breeding for resistance to potato leafroll virus in potato, p. 69–73. In: A. G. B. Beekman, K. M. Louwes, L. M. W. Dellaert, and A. E. F. Neele (eds). *Potato research of tomorrow*. Pudoc, Wageningen.
- Pfannenstiel, M. A., and S. A. Slack. 1980. Response of potato cultivars to the infection by the potato spindle tuber viroid. *Phytopathology* 70:922–926.
- Pfeffer, C., and M. Effmert. 1985. Die Züchtung homozygoter Eltern für Resistenz gegen Kartoffelschorf, verursacht durch *Streptomyces scabies* (Thaxt.) Waksman et Henrici (Breeding of homozygous parents for resistance to common potato scab caused by *Streptomyces scabies* (Thaxt.) Waksman et Henrici). *Arch. Züchtungsforschung* 15:325–333.
- Pfeffer, C., and M. Effmert. 1986. Die Eignung von Feldprüfungen und Gewächshausprüfungen zur Bewertung der Resistenz gegen Kartoffelschorf, verursacht durch *Streptomyces scabies* (Applicability of field and greenhouse testing to assessment of resistance to common potato scab caused by *Streptomyces scabies*). *Arch. Züchtungsforschung* 16:253–262.
- Phillips, M. S. 1981. A method of assessing potato seedling progenies for resistance to the white potato cyst nematode. *Potato Res.* 24:101–103.
- Phillips, M. S., and M. F. B. Dale. 1982. Assessing potato seedling progenies for resistance to the white potato cyst-nematode. *J. Agr. Sci. (Camb.)* 99:67–70.
- Phillips, M. S., and D. L. Trudgill. 1985. Pot and field assessment of partial resistance of potato clones to different populations and densities of *Globodera pallida*. *Nematologica* 31:433–442.
- Phillips, M. S., D. L. Trudgill, and K. Evans. 1988. The use of single, spaced potato plants to assess their tolerance of damage by potato cyst nematodes. *Potato Res.* 31:469–475.
- Phillips, M. S., L. A. Wilson, and J. M. S. Forrest. 1979. General and specific combining ability of potato parents for resistance to the white potato cyst nematode (*Globodera pallida*). *J. Agr. Sci., Camb.* 92:255–256.
- Pimentel, D., and L. Levitan. 1986. Pesticides: Amounts applied and amounts reaching pests. *BioScience* 36:86–91.
- Plaisted, R. L. 1957. Some components of the variance of specific gravity of potatoes. *Proc. Am. Soc. Hort. Sci.* 70:391–396.
- Plaisted, R. L. 1980. Potato, p. 483–494. In: W. R. Fehr and H. H. Hadley (eds.), *Hybridization of crop plants*. Am. Soc. Agronomy—Crop Science Soc. of Am., Madison, WI.
- Plaisted, R. L. 1983. Population breeding applied to improvement of unadapted *Solanum* cultivated species, p. 143–162. In: *Present and future strategies for potato breeding and improvement*. Rpt. 26th Planning Conf. Int. Potato Center, Lima, Peru.
- Plaisted, R., and A. Cubillos. 1972. Selection of parents on the basis of components of yield. *Am. Potato J.* 49:182–186.
- Plaisted, R. L., and R. W. Hoopes. 1989. The past record and future prospects for the use of exotic potato germplasm. *Am. Potato J.* 66:603–627.
- Plaisted, R. L., and L. C. Peterson. 1959. A technique for evaluating the ability of selections to yield consistently in different locations or seasons. *Am. Potato J.* 36:381–385.
- Plaisted, R. L., L. Sanford, W. T. Federer, A. E. Kehr, and L. C. Peterson. 1962. Specific and general combining ability for yield in potatoes. *Am. Potato J.* 39:185–197.
- Plaisted, R. L., H. D. Thurston, B. B. Brodie, and R. W. Hoopes. 1984. Selecting for resistance to diseases in early generations. *Am. Potato J.* 61:395–403.
- Plaisted, R. L., H. D. Thurston, J. B. Sieczka, B. B. Brodie, E. D. Jones, and R. C. Cetas. 1981. Rosa: A new golden nematode resistant variety for chipping and tablestock. *Am. Potato J.* 58:451–455.
- Platt, H. W. 1987. Potato late blight and its control, p. 271–286. In: G. Boiteau, R. P. Singh, and R. H. Parry (eds.), *Potato pest management in Canada*. Proc. Symp. Improving

- Potato Pest Production in Canada, Fredericton, N. B., Jan. 1987.
- Platt, H. W., and J. B. Sanderson. 1987. Comparison of inoculation methods for field studies on varietal response to verticillium wilt of potatoes. *Am. Potato J.* 64:87-92.
- Platt, H. W., and G. C. C. Tai. 1984. Assessment and analyses for the interpretation of potato late blight response in field studies. *Am. Potato J.* 61:599-609.
- Powell, W., J. Brown, and P. D. S. Caligari. 1989. Variability in response of potato cultivars to micropropagation. II. Subsequent field performance. *Ann. Appl. Biol.* 115:123-128.
- Powell, W., and H. Uhrig. 1987. Anther culture of *Solanum* genotypes. *Plant Cell, Tissue Organ Cult.* 11:13-24.
- Prakash, J. and M. J. Foxe. 1985. Optimisation of conditions for infection of isolated potato protoplasts with potato virus X. *Arch. Virol.* 85:269-279.
- Prasad, B., and B. B. Nagaich. 1983. Screening potato varieties for multiple resistance to *Phoma*, *Alternaria* and *Phytophthora* blights. *Ind. J. Agr. Sci.* 53:1043-1045.
- Preťová, A., and B. Dedičová. 1990. Somatic embryogenesis from unripe *Solanum tuberosum* (cv. Désirée) embryos. *Abstr. VII Intl. Congr. on Plant Tissue and Cell Culture*, Amsterdam, June 1990, p. 265.
- Proudfoot, K. G. 1969. The present status of breeding varieties resistant to potato wart and golden nematode in Newfoundland. *Proc. 4th Triennial Conf. Eur. Assoc. for Potato Res.*, Brest, France, p. 139-140.
- Proudfoot, K. G. 1976. Potato wart disease in Newfoundland. *Eur. Plant Prot. Org. Bull.* 6:225-229.
- Puite, K. J., and W. M. Mattheij. 1989. Somatic hybrid plants from 2x (+) 2x fusions between *Solanum tuberosum* and *S. phureja*, p. 96-101. In: K. M. Louwes, H. A. J. M. Toussaint, and L. M. W. Dellaert (compilers), *Parental line breeding and selection in potato breeding*. *Proc. joint Conf. EAPR-EUCARPIA*, Wageningen, Dec. 1988. Pudoc, Wageningen.
- Pushkarnath, and H. S. Chauhan. 1964a. Effect of gibberellic acid and temperature treatments on flowering and seed setting in some potato varieties. *Indian Potato J.* 6:90-95.
- Pushkarnath, and H. S. Chauhan. 1964b. Histology of floral abscission in potato. *Indian Potato J.* 6:7-12.
- Quraishi, A., and I. John. 1985. Organogenetic callus formation from various potato explants. *Pakistan J. Agr. Res.* 6:271-273.
- Radcliffe, E. B. 1982. Insect pests of potato. *Annu. Rev. Entomol.* 27:173-204.
- Radcliffe, E. B., and F. I. Lauer. 1968. Resistance to *Myzus persicae* (Sulzer), *Macrosiphum euphorbiae* (Thomas), and *Empoasca fabae* (Harris) in the wild tuber-bearing *Solanum* (Tourn.) L. species. *Tech. Bull.* 259. Univ. Minnesota Agr. Expt. Sta.
- Radtke, W., and A. Escande. 1975. Vergleichende Untersuchungen über verschiedene Methoden zur Inokulation von Kartoffelsämlingen mit *Fusarium solani* (Mart.) Sacc. f. sp. *eumartii* (Carp.) Snyder et Hansen (Comparative studies of different methods of inoculating potato seedlings with *Fusarium solani* (Mart.) Sacc. f. sp. *eumartii* (Carp.) Snyder et Hansen). *Potato Res.* 18:243-255.
- Rahimi, F. R., and C. D. Carter. 1989. Prevention of flower abscission after pollination in *Solanum tuberosum* cv. Katahdin. *Am. Potato J.* 66:47-51.
- Ramanna, M. S. 1979. A re-examination of the mechanisms of 2n gamete formation in potato and its implications for breeding. *Euphytica* 28:537-561.
- Ramanna, M. S. 1983. First division restitution gametes through fertile desynaptic mutants of potato. *Euphytica* 32:337-350.
- Ramanna, M. S., and J. G. Th. Hermesen. 1979. Genome relationships in tuber-bearing *Solanums*, p. 647-654. In: J. G. Hawkes, R. N. Lester, and A. D. Skelding (eds.), *The biology and taxonomy of the Solanaceae*. *Linn. Soc. Symp.*, Ser. 7. Academic Press, London.

- Ramanna, M. S., and J. G. Th. Hermesen. 1982. Gene transfer from non-tuberosus to tuberosus *Solanum* species: Evidence from meiosis in hybrids. *Euphytica* 31:565–572.
- Rasco, E. T. Jr., R. L. Plaisted, and E. E. Ewing. 1980. Photoperiod response and earliness of *S. tuberosum* ssp. *andigena* after six cycles of recurrent selection for adaptation to long days. *Am. Potato J.* 57:435–447.
- Reeves, A. F. II. 1988. Varietal differences in potato tuber greening. *Am. Potato J.* 65:651–658.
- Reifschneider, F. J. B., C. M. T. Cordeiro, and F. A. R. Filgueira. 1986. Resistência de batata a *Alternaria solani* (Resistance of potato to *Alternaria solani*) *Hort. Brasileira* 4:22–25.
- Reifschneider, F. J. B., C. M. T. Cordeiro, F. A. R. Filgueira, C. Bittencourt, and M. E. N. Fonseca. 1985. Avaliação do da resistência de germoplasma de batata (*Solanum* spp.) a *Alternaria solani* (Evaluation of potato [*Solanum* spp.] germplasm for resistance to *Alternaria solani*). *Fitopatol. Bras.* 10:597–604.
- Reifschneider, F. J., O. Furumoto, and F. A. R. Filgueira. 1984. Illustrated key for the evaluation of early blight of potatoes. *FAO Plant Prot. Bull.* 32:91–94.
- Reust, W. 1986. EAPR working group 'physiological age of the potato'. *Potato Res.* 29:268–271.
- Rex, B. L., and G. Mazza. 1989. Cause, control and detection of hollow heart in potatoes: A review. *Am. Potato J.* 66:165–183.
- Richardson, D. E. 1979. Potato variety testing at the NIAB. *J. Nat. Inst. Agr. Bot.* 15:92–97.
- Rietveld, R. C., P. M. Hasegawa, and R. A. Bressan. 1987. Genetic variability in tuber derived potato plants, 392–407. In: Y. P. S. Bajaj (ed.), *Biotechnology in agriculture and forestry*. Vol. 3: Potato. Springer-Verlag, Berlin.
- RIVRO. 1990. 65e Beschrijvende rassenlijst voor landbouwgewassen 1990 (65th descriptive list of cultivars of agricultural crops 1990). RIVRO, Bennekon, NL.
- Rizvi, S. A. H., and K. V. Raman. 1983. Effects of glandular trichomes on the spread of potato virus Y (PVY) and potato leafroll virus (PLRV) in the field, p. 162–163. In: W. J. Hooker (ed.), *Research for the potato in the year 2000*. Int. Potato Center, Lima, Peru.
- Roath, W. W. 1989. Evaluation and enhancement. *Plant Breed. Rev.* 7:183–211.
- Roddick, J. G. 1986. Steroidal alkaloids of the Solanaceae, p. 202–222. In: W. G. D'Arcy (ed.), *Solanaceae: Biology and systematics*. Columbia Univ. Press, New York.
- Roos, E. E. 1980. Physiological, biochemical, and genetic changes in seed quality during storage. *HortScience* 15:781–784.
- Rosahl, S., R. Schmidt, J. Schell, and L. Willmitzer. 1986. Isolation and characterization of a gene from *Solanum tuberosum* encoding patatin, the major storage protein of potato tubers. *Mol. Gen. Genet.* 203:214–220.
- Ross, H. 1977. Methods for breeding virus resistant potatoes, p. 93–114. In: *Rept. Planning Conf. Dev. Control Potato Virus Dis.* Int. Potato Center, Lima, Peru.
- Ross, H. 1983. Major and minor genes in breeding virus resistant varieties, p. 165–166. In: W. J. Hooker (ed.), *Research for the potato in the year 2000*. Int. Potato Center, Lima, Peru.
- Ross, H. 1986. Potato breeding—Problems and perspectives. *Advances in Plant Breeding*. Suppl. 13. J. Plant Breed. Verlag, Paul Parey, Berlin.
- Ross, H., P. Pasemann, and W. Nitzsche. 1978. Der Glykoalkaloidgehalt von Kartoffelsorten in seiner Abhängigkeit von Anbauort und—jahr und seiner Beziehung zum Geschmack (The glycoalkaloid content of potato varieties in relation to place and year of cultivation and to flavour). *Z. Pflanzenzüchtg.* 80:64–79.
- Ross, R. W., J. E. Smejkal, and R. E. Hanneman, Jr. 1980. Gibberellin induced flowering in two hard-to-flower tuber-bearing *Solanum* species. *Am. Potato J.* 57:490–491 (Abstr.)

- Rothacker, D., and B. Effmert. 1968. Zur Problematik der züchterischen Veränderung des Amylose: Amylopektin-Verhältnisses der Kartoffellstärke (On the problem of change in the proportions of amylose/amylopectin in potato starch through breeding). *Theor. Appl. Genet.* 38:309-313.
- Rowe, R. C. 1985. Potato early dying—A serious threat to the potato industry. *Am. Potato J.* 62:157-161.
- Rowe, R. C., J. R. David, M. L. Powelson, and D. I. Rouse. 1987. Potato early dying: Causal agents and management. *Plant Dis.* 71:482-489.
- Russell, G. E. 1978. Plant breeding for pest and disease resistance. *Studies in the agricultural and food sciences*. Butterworths, London.
- Salazar, L. F. 1989. Potato spindle tuber, p. 155-167. In: R. P. Kahn (ed.), *Plant protection and quarantine. II. Selected pests and pathogens of quarantine significance*. CRC Press, Boca Raton, FL.
- Salunkhe, D. K., B. B. Desai, and J. K. Chavan. 1989. Potatoes, p. 1-52. In: N. A. M. Eskin (ed.), *Quality and preservation of vegetables*. CRC Press, Boca Raton, FL.
- Samotus, B., M. Leja, A. Scigalski, J. Dulinski, and R. Siwanowicz. 1986. Analytical remarks to explain some discrepancies in the determination of dry matter and starch from potato tubers density. *Starch/Stärke* 38:14-19.
- Sampson, P. J. 1983. Resistance in potato to powdery scab, due to *Spongospora subterranea*, p. 169. In: W. J. Hooker (ed.), *Research for the potato in the year 2000*. Int. Potato Center, Lima, Peru.
- Sanford, J. C., and R. E. Hanneman, Jr. 1979. Reciprocal differences in the photoperiod reaction of hybrid populations in *Solanum tuberosum*. *Am. Potato J.* 56:531-540.
- Sanford, J. C., and R. E. Hanneman, Jr. 1981. The use of bees for the purpose of inter-mating in potato. *Am. Potato J.* 58:481-485.
- Sanford, J. C., and R. E. Hanneman, Jr. 1982. Large yield differences between reciprocal families of *Solanum tuberosum*. *Euphytica* 31:1-12.
- Sanford, L. L. 1960. Comparative evaluation of clones as testers for yield, specific gravity and tuber appearance in the potato. Ph.D Thesis, Iowa State Univ., Ames, Iowa.
- Sanford, L. L., and T. L. Ladd, Jr. 1987a. Recurrent selection for potato leafhopper resistance in potato, *Solanum tuberosum* L. Gp. *Tuberosum*. *Am. Potato J.* 64:367-375.
- Sanford, L. L., and T. L. Ladd, Jr. 1987b. Genetic transmission of potato leafhopper resistance from recurrent selection populations in potato *Solanum tuberosum* L. Gp. *Tuberosum*. *Am. Potato J.* 64:655-662.
- Sanford, L. L., T. L. Ladd, S. L. Sinden, and W. W. Cantelo. 1984. Early generation selection of insect resistance in potato. *Am. Potato J.* 61:405-418.
- Schenk, G., and K. Neitzel. 1985. A contribution to the maintenance of phytopathogenic virus strains on tissue culture plantlets. *Potato Res.* 28:535-538.
- Schiessendoppler, E. 1987. Methoden zur Prüfung der sortenspezifischen Anfälligkeit gegenüber den Erregern der Dürffleckenkrankheit des Kartoffellaubes und der Hartfäule der Knolle (*Alternaria solani* (Ell. & Mart.) Jones & Grouet und *A. alternata* (Fries) Keissler), p. 36-38. In: *Potato disease assessment keys*. Eur. Assoc. for Potato Res., Section for Pathology.
- Schittenhelm, S. 1989. Use of neo-tuberosum clones as parents in a starch potato breeding programme, p. 143-147. In: K. M. Louwes, H. A. J. M. Toussaint, and L. M. W. Dellaert (compilers), *Parental line breeding and selection in potato breeding*. Proc. joint Conf. EAPR-EUCARPIA, Wageningen, Dec. 1988. Pudoc, Wageningen.
- Schneider, F. 1986. The concept of distinctness in plant breeders' rights, p. 393-397. In: B. J. Styles (ed.), *Intraspecific classification of wild and cultivated plants*. Syst. Assoc. Spec. Vol. 29.
- Schöber, B. 1987a. Beurteilung und Erfassung von Braunfäule (*Phytophthora infestans*

- (Mont.) de Bary) in den Knollen, p. 28-35. In: Potato disease assessment keys. Eur. Assoc. for Potato Res., Section for Pathology.
- Schöber, B. 1987b. Methoden zur Prüfung der Anfälligkeit von Kartoffelknollen für den gewöhnlichen Schorf *Streptomyces scabies* (Thaxt.) Waksman et Henrici, p. 73-82. In: Potato disease assessment keys. Eur. Assoc. for Potato Res., Section for Pathology.
- Schöber, B. 1987c. *Phytophthora infestans* (Mont.) de Bary—eine ständige Herausforderung seit 140 Jahren (*Phytophthora infestans* (Mont.) de Bary—A permanent challenge since 140 years). Ber. Deutsch. Bot. Ges. 100:291-303.
- Schöber, B., and E. Schiessendoppler. 1987. Some interesting aspects of recent and expected developments of diseases and pests and their control in Europe, p. 169-174. In: Hesen, J. C., C. D. Van Loon, J. G. Th. Hermesen, and L. J. Turkensteen (eds.), Recent and future developments of the potato in the world. Workshop, April 1987. Acta Hort. 213.
- Schumacher, J., N. Meyer, D. Riesner, and H. L. Weidemann. 1986. Diagnostic procedure for detection of viroids and viruses with circular RNAs by "return"-gel electrophoresis. J. Phytopathol. 115:332-343.
- Scott, R. K., and S. J. Wilcockson. 1982. Application of physiological and agronomic principles to the development of the potato industry, p. 678-704. In: P. M. Harris (ed.), The potato crop. Chapman & Hall, London.
- Seabrook, J. E. A. and S. Coleman. 1988. Guidelines for shipping *in vitro* potato plantlets. Am. Potato J. 65:301-308.
- Seabrook, J. E. A., and L. K. Douglass. 1990. Embryo culture of potato (*Solanum tuberosum* L.). Am. Potato J. 67:575-576 (Abstr.).
- Secor, G. A., and J. F. Shepard. 1981. Variability of protoplast-derived potato clones. Crop Sci. 21:102-105.
- Seinhorst, J. W. 1984. Relation between population density of potato cyst nematodes and measured degrees of susceptibility (resistance) of resistant potato cultivars and between this density and cyst content in the new generation. Nematologica 30:66-76.
- Sekioka, T. T., and F. I. Lauer. 1970. Some estimates of genotype X environment interactions in potato variety tests. Am. Potato J. 47:304-310.
- Seppänen, E. 1981. Fusariums of the potato in Finland. III. Varietal resistance of potato tubers to some *Fusarium* species. Ann. Agr. Fenn. 20:177-183.
- Seppänen, E. 1982. Further studies on varietal differences in resistance to potato gangrene. Ann. Agr. Fenn. 22:155-161.
- Sharma, R., and R. H. Cammack. 1976. A modification of the Glynne-Lemmerzahl method for testing resistance of potato varieties to wart disease, *Synchytrium endobioticum*. (Schilb.) Perc. Potato Res. 19:165-167.
- Shaw, D. S. 1987. The breeding system of *Phytophthora infestans*: The role of the A₂ mating type, p. 161-174. In: P. R. Day and G. J. Jellis (eds.) Genetics and plant pathogenesis. Blackwell Scientific, Boston.
- Sidhu, A. S., and M. L. Pandita. 1980. Genetic divergence for yield and its components in potato (*Solanum tuberosum* L.). Genet. Agr. 34:235-244.
- Sidhu, A. S., M. L. Pandita, and S. K. Arora. 1984. A study of variation in potato varieties and advanced hybrids. Haryana agric. Univ. J. Res., Vol. XIV:476-479.
- Sieczka, M. T. 1989. Progress in the development of potato clones with multiple resistance to pathogenes and pests, p. 205. In: K. M. Louwes, H. A. J. M. Toussaint, and L. M. W. Dellaert (compilers), Parental line breeding and selection in potato breeding. Proc. joint Conf. EAPR-EUCARPIA, Wageningen, Dec. 1988. Pudoc, Wageningen.
- Simmonds, N. W. 1966. Studies of the tetraploid potatoes. 3. Progress in the experimental re-creation of the Tuberosum Group. J. Linn. Soc. (Bot.) 59:279-288.
- Simmonds, N. W. 1969. Prospects of potato improvement, p. 18-38. In: Scottish Soc. Res. Plant Breed. Annu. Meet. Scottish Plant Breeding Station, Pentlandsfield.

- Simmonds, N. W. 1976. Potatoes, p. 279-283. In: N. W. Simmonds, Evolution of crop plants. Longman, New York.
- Simmonds, N. W. 1979. Principles of crop improvement. Longman, London and New York.
- Simmonds, N. W. 1980. Comparisons of the yields of four potato varieties in trials and in agriculture. *Expt. Agr.* 16:393-398.
- Simmonds, N. W., and R. L. Wastie. 1987. Assessment of horizontal resistance to late blight of potatoes. *Ann. Appl. Biol.* 111:213-221.
- Sinden, S. L., K. L. Deahl, and B. B. Aulenbach. 1976. Effect of glycoalkaloids and phenolics on potato flavor. *J. Food Sci.* 41:520-523.
- Sinden, S. L., R. W. Goth, and M. J. O'Brien. 1973. Effect of potato alkaloids on the growth of *Alternaria solani* and their possible role as resistance factors in potatoes. *Phytopathology* 63:303-307.
- Sinden, S. L., L. L. Sanford, and S. F. Osman. 1980. Glycoalkaloids and resistance to the Colorado potato beetle in *Solanum chacoense*. *Bitter. Am. Potato J.* 57:331-343.
- Sinden, S. L., L. L. Sanford, and R. E. Webb. 1984. Genetic and environmental control of potato glycoalkaloids. *Am. Potato J.* 61:141-156.
- Sinden, S. L., and R. E. Webb. 1972. Effect of variety and location on the glycoalkaloid content of potatoes. *Am. Potato J.* 49:334-338.
- Sinden, S. L., R. E. Webb, and L. L. Sanford. 1978. Genetic potential for increasing ascorbic acid content in potatoes. *Am. Potato J.* 55:394-395.
- Singh, A. K., J. P. Moss, and J. Smartt. 1990. Ploidy manipulations for interspecific gene transfer. *Adv. Agron.* 43:199-240.
- Singh, M. N., S. M. P. Khurana, and B. B. Nagaich. 1983. Evidence on heredity variations in the virus transmission efficiency of aphid clones. *Z. Pflanzenkrankh. Pflanzensch.* 90:345-351.
- Singh, R. P. 1986. Occurrence, diagnosis and eradication of the potato spindle tuber viroid from Canada, p. 37-50. In: Viroids of plants and their detection. *Proc. Int. Seminar, Warsaw Agr. Univ.*
- Singh, R. P., and A. Boucher. 1988. Comparative detection of mild strains of potato spindle tuber viroid from dormant potato tubers by return polyacrylamide gel electrophoresis and nucleic acid hybridization. *Potato Res.* 31:159-166.
- Singh, R. P., A. Boucher, and J. E. A. Seabrook. 1988. Detection of the mild strains of potato spindle tuber viroid from single true potato seed by return electrophoresis. *Phytopathology* 78:663-667.
- Singh, R. P., and S. Slack. 1984. Reactions of tuber bearing *Solanum* species to infection with potato spindle tuber viroid. *Plant Dis.* 68:784-787.
- Singh, R. P., and T. H. Somerville. 1987. Relationship of virus concentration with the field resistance to potato virus Y in potatoes. *Am. Potato J.* 64:69-80.
- Skrobacki, A., J. L. Halderson, J. J. Pavsek, and D. L. Corsini. 1989. Determining potato tuber resistance to impact damage. *Am. Potato J.* 66:401-415.
- Sleesman, J. P., and F. J. Stevenson. 1941. Breeding a potato resistant to the potato leafhopper. *Am. Potato J.* 18:280-298.
- Smith, O. 1987a. Effect of cultural and environmental conditions on potatoes for processing, p.73-147. In: W. F. Talburt and O. Smith (eds.), *Potato processing*. 4th ed. Van Nostrand Reinhold, New York.
- Smith, O. 1987b. Potato chips, p. 371-489. In: W. F. Talburt and O. Smith (eds.), *Potato processing*. 4th ed. Van Nostrand Reinhold, New York.
- Sneath, P. H. A. 1976. Some applications of numerical taxonomy to plant breeding. *Z.Pflanzenzücht.* 76:19-46.
- Snowcroft, W. R. 1984. Genetic variability in tissue culture: Impact on germplasm conservation and utilization. IBPGR Report, Int. Board for Plant Genetic Resources,

- FAO, Rome.
- Sonnino, A., G. Ancora, and C. Locardi. 1986. *In vitro* mutation breeding of potato. Use of propagation by microcuttings. Proc. Int. Symp. Nuclear techniques and *in vitro* culture for plant improvement. IAEA-SM. Vienna, 19-23 Aug. 1985. p. 385-394.
- Sonnino, A., S. Tanaka, M. Iwanaga, and L. Schilde-Rentschler. 1989. Genetic control of embryo formation in anther culture of diploid potatoes. Plant Cell Rep. 8:105-107.
- Sonnino, A., R. Tavazza, V. Beinat, and G. Ancora. 1987. Variability in protoplast-derived plants as compared to variability induced by *in-vitro* irradiation of shoots. Proc. 10th Trien. Conf. Eur. Assoc. for Potato Res., July 1987. European Assoc. Potato Res. Aalborg, Denmark.
- Sopory, S. K., E. Jacobsen, and G. Wenzel. 1978. Production of monohaploid embryoids and plantlets in cultured anthers of *Solanum tuberosum*. Plant Science Lett. 12:47-54.
- Sowokinos, J. R. 1978. Relationship of harvest sucrose content to processing maturity and storage life of potatoes. Am. Potato J. 55:333-344.
- Spitters, C. J. T., A. E. F. Neele, and A. H. C. M. Schapendonk. 1989. Crop physiological components of tuber yield and their use in potato breeding, p. 51-60. In: K. M. Louwes, H. A. J. M. Toussasint, and L. M. W. Dellaert (compilers), Parental line breeding and selection in potato breeding. Proc. joint Conf. EAPR-EUCARPIA, Wageningen, Dec. 1988.
- Spooner, D. M., J. Bamberg, J. P. Hjerting, and J. Gomez. 1991. Mexico: 1988 potato collecting expedition and utility of the Mexican species. Am. Potato J. 68:29-43.
- Sree Ramulu, K. S., P. Dijkhuis, and S. Roest. 1989. Patterns of phenotypic and chromosome variation in plants derived from protoplast cultures of monohaploid, dihaploid and diploid genotypes and in somatic hybrids of potato. Plant Sci. 60:101-110.
- Sree Ramulu, K., P. Dijkhuis, S. Roest, G. S. Bokelmann, and B. de Groot. 1986. Variation in phenotype and chromosome number of plants regenerated from protoplasts of dihaploid and tetraploid potato. Plant Breed. 97:119-128.
- Stegemann, H., and V. Loeschcke. 1976. Index of European potato varieties. Mitt. Biol. Bundesanst. Land. Forstwirtschaft. Berl.-Dahlem. Paul Parey, Berlin. 168:1-215.
- Stegemann, H., and D. Schnick. 1985. Index 1985 of European varieties. Mitt. Biol. Bundesanst. Land. Forstwirtschaft. Berl.-Dahlem, Paul Parey, Berlin.
- Stelly, D. M., and S. J. Peloquin. 1986. Formation of 2n megagametophytes in diploid tuber-bearing *Solanums*. Am. J. Bot. 73:1351-1363.
- Stewart, H. E., P. H. Flavelle, D. C. McCalmont, and R. L. Wastie. 1983a. Correlation between glass house and field tests for resistance to foliage blight caused by *Phytophthora infestans*. Potato Res. 26:41-48.
- Stewart, H. E., D. C. McCalmont, and R. L. Wastie. 1983b. The effect of harvest date and the interval between harvest and inoculation on the assessment of the resistance of potato tubers to late blight. Potato Res. 26:101-107.
- Stewart, H. E., K. Taylor, and R. L. Wastie. 1983c. Resistance to late blight in foliage (*Phytophthora infestans*) of potatoes assessed as true seedlings and as adult plants in the glasshouse. Potato Res. 26:363-366.
- Stiekema, W. J., F. Heidekamp, J. D. Louwerse, H. A. Verhoeven, and P. Dijkhuis. 1988. Introduction of foreign genes into potato cultivars Bintje and Désirée using an *Agrobacterium tumefaciens* binary vector. Plant Cell Rep. 7:47-50.
- Stone, A. R. 1987. Genetic systems in plant pathogenic nematodes and their hosts, p. 101-109. In: P. R. Day and G. J. Jellis (eds.), Genetics and plant pathogenesis. Blackwell, Boston.
- Storey, R. M. J., and R. J. Marks. 1983. Screening for resistance to potato cyst nematodes using bioluminescent photometry. Ann. Appl. Biol. 103:321-326.
- Susnoschi, M., J. Krikun, and Z. Zuta. 1976. Trial of common potato varieties in relation to

- their susceptibility to verticillium wilt. *Potato Res.* 19:323-334.
- Świeżyński, K. M. 1978. Selection of individual tubers in potato breeding. *Theor. Appl. Genet.* 53:71-80.
- Świeżyński, K. M. 1984. Early generation selection methods used in Polish potato breeding. *Am. Potato J.* 61:385-394.
- Świeżyński, K. M. 1987. Some interesting aspects of potato breeding in Europe, p. 51-59. In: J. C. Heslen, C. D. Van Loon, J. G. Hermesen, and L. J. Turkensteen (eds.), *Recent and future developments of the potato in the world. Workshop, April 1987, Wageningen. Acta Hort.* 213.
- Świeżyński, K. M., A. Sykala, and J. K. Wroblewska. 1978. Differences in early growth of shoots and roots in potato clones. *Potato Res.* 21:241-248.
- Tai, G. C. C. 1971. Genotypic stability analysis and its application to potato regional trials. *Crop Sci.* 11:184-190.
- Tai, G. C. C. 1974. A method for quantitative genetic analysis of early clonal generation seedlings of an asexual crop with special application to a breeding population of the potato (*Solanum tuberosum* L.). *Theor. Appl. Genet.* 45:150-156.
- Tai, G. C. C. 1975a. Effectiveness of visual selection for early clonal generation seedlings of potato. *Crop Sci.* 15:15-18.
- Tai, G. C. C. 1975b. Analysis of genotype-environment interactions based on the method of path coefficient analysis. *Can. J. Genet. Cytol.* 17:141-149.
- Tai, G. C. C. 1976. Estimation of general and specific combining abilities in potato. *Can. J. Genet. Cytol.* 18:463-470.
- Tai, G. C. C. 1979. Analysis of genotype-environment interactions of potato yield. *Crop Sci.* 19:434-438.
- Tai, G. C. C. 1989. Biometrical methods in investigating 2n gametes in tetraploid-diploid and diploid-diploid crosses, p. 15-21. In: K. M. Louwes, H. A. J. M. Toussaint, and L. M. W. Dellaert (compilers), *Parental line breeding and selection in potato breeding. Proc. joint Conf. EAPR-EUCARPIA, Wageningen, Dec. 1988. Pudoc, Wageningen.*
- Tai, G. C. C., and H. De Jong. 1980. Multivariate analyses of potato hybrids. I. Discrimination between tetraploid-diploid hybrid families and their relationship to cultivars. *Can. J. Genet. Cytol.* 22:227-235.
- Tai, G. C. C. and W. A. Hodgson. 1975. Estimating general combining ability of potato parents for field resistance to late blight. *Euphytica* 24:285-289.
- Tai, G. C. C., and T. R. Tarn. 1980. Multivariate analyses of potato hybrids. II. Discrimination between *Tuberosum*-*Andigena* hybrid families and their relationship to their parents. *Can. J. Genet. Cytol.* 22:279-286.
- Tai, G. C. C., P. Y. Jui, and D. A. Young. 1986. Evaluation of parents based on long-term selection records. *Z. Pflanzenzücht.* 96:39-46.
- Tai, G. C. C., G. C. Misener, E. S. Allaby, and L. P. McMillan. 1985. GRAV-O-TATER: A computerized apparatus for measuring specific gravity. *Am. Potato J.* 62:403-408.
- Tai, G. C. C., and D. A. Young. 1972. Genotypic stability analysis of eight potato varieties tested in a series of ten trials. *Am. Potato J.* 49:138-150.
- Tai, G. C. C., and D. A. Young. 1984. Early generation selection for important agronomic characteristics in a potato breeding population. *Am. Potato J.* 61:419-434.
- Tai, G. C. C., and D. A. Young. 1989. Performance and prediction of potato genotypes tested in international trials. *Euphytica* 42:275-284.
- Talbur, W. F., S. Schwimmer, and H. K. Burr. 1987. Structure and chemical composition of the potato tuber, p. 11-46. In: W. F. Talbur and O. Smith (eds.), *Potato processing*, 4th ed. Van Nostrand Reinhold, New York.
- Tarn, T. R. 1981. Changes in *Solanum tuberosum* Group *Andigena* during five cycles of recurrent mass selection. *Am. Potato J.* 58:521 (Abstr.).
- Tarn, T. R. 1987. The potential of plant resistance for insect control. In: G. Boiteau,

- R. P. Singh, and R. H. Parry. Potato pest management in Canada. Proc. Symp. Improving Potato Pest Protection, Fredericton, N. B., Jan. 1987, p. 224-241.
- Tarn, T. R., A. Rivera Peña, J. P. Hjerting, R. W. Ross, and J. Gomez. 1985. Potato collecting in Mexico. Am. Potato J. 62:442-443 (Abstr.).
- Tarn, T. R., and G. C. C. Tai. 1977. Heterosis and variation of yield components in F_1 hybrids between Group Tuberosum and Group Andigena potatoes. Crop Sci. 17:517-521.
- Tarn, T. R., and G. C. C. Tai. 1983. Tuberosum $\times$ Tuberosum and Tuberosum $\times$ Andigena potato hybrids: Comparisons of families and parents and breeding strategies for Andigena potatoes in long-day temperate environments. Theor. Appl. Genet. 66:87-91.
- Tavazza, R., M. Tavazza, R. J. Ordas, G. Ancora, and E. Benvenuto. 1988. Genetic transformation of potato (*Solanum tuberosum*): An efficient method to obtain transgenic plants. Plant Sci. 59:175-181.
- Tegera, P., and G. Fouarge. 1984. Comparaison entre les evaluations en champ, en serre et au laboratoire de la resistance du feuillage et des tubercules d'hybrids de pomme de terre a l'egard du *Phytophthora infestans* (Mont.) de Bary (Comparison between field, greenhouse and laboratory evaluation of haulm and tuber resistance of potato hybrids against *Phytophthora infestans* (Mont.) de Bary). Med. Fac. Landbouww. Rijksuniv. (Gent.) 36:227-235.
- Thomas, E., S. W. J. Bright, J. Franklin, V. A. Lancaster, and B. J. Mifflin. 1982. Variation amongst protoplast-derived potato plants (*Solanum tuberosum* cv. 'Maris Baird'). Theor. Appl. Genet. 62:65-68.
- Thompson, P. G., F. L. Haynes, and R. H. Moll. 1980. Estimation of genetic variance components and heritability for tuber dormancy in diploid potatoes. Am. Potato J. 57:39-46.
- Thurston, H. D. 1978. Potentialities for pest management in potatoes, p. 117-136. In: Pest control strategies. Academic Press, New York.
- Thurston, H. D. 1979. Breeding for late blight resistance. In: Proc. Rice Blast Workshop. Internat. Rice Res. Inst., Los Baños, Philippines, p. 141-152.
- Tingey, W. M. 1981. Potential for plant resistance in management of arthropod pests, p. 268-288. In: J. H. Lashomb and R. Casagrande (eds.), Advances in potato pest management. Hutchinson Ross Publ., Stroudsburg, PA.
- Tingey, W. M. 1984. Glycoalkaloids as pest resistance factors. Am. Potato J. 61:157-167.
- Tingey, W. M. 1986. Techniques for evaluating plant resistance to insects, p. 251-284. In: J. R. Miller and T. A. Miller (eds.), Insect-plant interactions. Springer-Verlag, New York.
- Tingey, W. M., and J. E. Laubengayer. 1986. Glandular trichomes of a resistant hybrid potato alter feeding behaviour of the potato leafhopper (Homoptera: Cicadellidae). J. Econ. Entomol. 79:1230-1234.
- Torka, M. 1958. Resistenzzüchtung gegen den Kartoffelkäfer (Breeding for resistance to the [Colorado] potato beetle.), p. 125-128. In: H. Kappert and W. Rudolf, Handbuch der Pflanzenzüchtung, vol. 3. Paul Parey, Berlin.
- Torres, G. J., J. M. Galan, and E. C. Diaz. 1974. Correlaciones geneticas e indices de seleccion en la genotecnica de la papa (*Solanum tuberosum* L.). Agrociencia 16:21-37.
- Towill, L. E. 1982. Low temperature (-196°C) storage of true seed from tuber-bearing *Solanum* species. Am. Potato J. 59:141-147.
- Towill, L. E. 1983. Longevity of true seed from tuber-bearing and closely related non-tuber-bearing *Solanum* species. Am. Potato J. 60:75-83.
- Towill, L. E. 1984. Survival at ultra-low temperatures of shoot tips from *Solanum tuberosum* groups Andigena, Phureja, Stenotomum, Tuberosum, and other tuber-bearing *Solanum* species. Cryo-Lett. 5:319-326.
- Toxopeus, H. J. 1952. On the possible significance of *Solanum demissum* in improving the yield of the cultivated potato. Euphytica 1:133-139.

- Toxopeus, H. J. 1953. On the significance of multiplex parental material in breeding for resistance to some diseases in the potato. *Euphytica*. 2:139-146.
- Trudgill, D. L. 1985. Potato cyst nematodes: A critical review of the current pathotyping scheme. *Eur. Plant Prot. Org. Bull.* 15:273-279.
- Tumer, N., C. Hemenway, K. O'Connell, M. Cuozzo, R. Fang, W. Kaniewski, and N. Chua. 1987. Expression of coat protein genes in transgenic plants confers protection against alfalfa mosaic virus, cucumber mosaic virus and potato virus X. *NATO Advanced Science Institute Series, Series A*, 140:351-356.
- Turkensteen, L. 1978. An overview of the important fungal pathogens of potatoes, p. 17-22. In: *Rpt. Planning Conf. Control Important Fungal Dis. Potatoes*. Int. Potato Center, Lima, Peru.
- Turkensteen, L. 1987. Silver scurf (*Helminthosporium solani* Dur. & Mont.) of potato tubers, p. 91-96. In: *Potato disease assessment keys*. Eur. Assoc. for Potato Res., Section for Pathology.
- Turner, A. D., and E. E. Ewing. 1988. Effects of photoperiod, night temperature, and irradiance on flower production in the potato. *Potato Res.* 31:257-268.
- Turner, S. J., A. R. Stone, and J. N. Perry. 1983. Selection of potato cyst—nematodes on resistant *Solanum vernei* hybrids. *Euphytica* 32:911-917.
- UPOV. 1986. Guidelines for the conduct of tests for distinctness, homogeneity and stability: Potato (*Solanum tuberosum* L.). Int. Union for the Prot. of New Varieties of Plants UPOV/TG/23/5. Geneva.
- Ugent, D. L., T. Dillehay, and C. Ramirez. 1987. Potato remains from a Late Pleistocene settlement in southcentral Chile. *Econ. Bot.* 41:17-27.
- Ugent, D. L., S. Pozorski, and T. Pozorski. 1982. Archaeological potato tuber remains from the Casma Valley of Peru. *Econ. Bot.* 36:182-192.
- Uhrig, H. 1985a. Breeding potatoes with dihaploids. *Eur. Plant Prot. Org. Bull.* 15:185-191.
- Uhrig, H. 1985b. Genetic selection and liquid medium conditions improve the yield of androgenetic plants from diploid potatoes. *Theor. Appl. Genet.* 71:455-460.
- Uhrig, H., and F. Salamini. 1987. Dihaploid plant production from 4x—genotypes of potato by the use of efficient anther plants producing tetraploid strains (4x EAPP—clones)—Proposal of a breeding methodology. *Plant Breeding*. 98:228-235.
- Umaerus, M. 1980. An integrated breeding program for yield, quality and resistance in potato. *Eur. Plant Prot. Org. Bull.* 10:385-391.
- Umaerus, M. 1986. Potato breeding for the future, p. 203-208. In: *Svalöf 1886-1986: Research and results in plant breeding*. Svalöf, A. B., Svalöv, Stockholm.
- Umaerus, V. 1987. Disease assessment of late blight (*Phytophthora infestans*) in the foliage, p. 21-27. In: *Potato disease assessment keys*. Eur. Assoc. for Potato Res., Section for Pathology.
- Umaerus, V., and D. Lihnell. 1976. A laboratory method for measuring the degree of attack by *Phytophthora infestans*. *Potato Res.* 19:91-107.
- Umaerus, V., M. Umaerus, L. Erjefält, and B. A. Nilsson. 1983. Control of *Phytophthora* by host resistance: Problems and progress, p. 315-326. In: D. C. Erwin, S. Bartnicki-Garcia, and P. H. Tsao (eds.), *Phytophthora, its biology, taxonomy, ecology and pathology*. Am. Phytopathol. Soc., St. Paul, MN.
- Upadhyia, M. D., M. J. Abraham, B. Dass, and R. Chandra. 1982. Mutation induction and isolation in potato through true seed and tuber mutagenesis and use of tissue culture. *Proc. Joint FAO/IAEA Div. Iso. Rad. Appl. Atom. Energy Food Agric. Dev. Induced mutations in vegetatively propagated plants*. II. 11-15 February, 1980, IAEA, Vienna. p. 185-198.
- Vanderplank, J. E. 1984. *Disease resistance in plants*, 2nd ed. Academic Press, New York.
- Van der Wal, A. F., W. F. Bouma, C. A. Huijsman, B. Maris, and N. J. Van Suchtelen. 1978. Breeding to maximize the physiological potential of potatoes for yield, p. 23-33. In:

- Survey papers. 7th Trien. Conf. Eur. Assoc. for Potato Res. Warsaw, Poland.
- Van der Zaag, D. E. 1987. Topics concerning potato research which require more international cooperation, p. 11–15. In: J. C. Heslen, C. D. Van Loon, J. G. Hermesen, and L. J. Turkensteen (eds.), Recent and future developments of the potato in the world. Workshop, April 1987, Wageningen. Acta Hort. 213.
- Van der Zaag, D. E., and W. G. Burton. 1978. Potential yield of the potato crop and its limitations, p. 7–22. In: Survey papers. 7th Trien. Conf. Eur. Assoc. for Potato Res. Warsaw, Poland.
- Van Gelder, W. M. J., J. H. Vinke, and J. J. C. Scheffer. 1988. Steroidal glycoalkaloids in tubers and leaves of *Solanum* species used in potato breeding. Euphytica 5:147–158.
- Van Gundy, S. D. 1985. Ecology of *Meloidogyne* spp.—Emphasis on environmental factors affecting survival and pathogenicity, p. 177–182. In: J. N. Sasser and C. C. Carter (eds.), An advanced treatise on *Meloidogyne*. Vol. 1. Biology and control. North Carolina State Univ. Graphics.
- Van Harten, A. M., H. Bouter, and C. Broertjes. 1981. In vitro adventitious bud techniques for vegetative propagation and mutation breeding of potato (*Solanum tuberosum* L.). II. Significance for mutation breeding. Euphytica 30:1–8.
- Van Harten, A. M., and C. Broertjes. 1989. Induced mutations in vegetatively propagated crops. Plant Breed. Rev. 6:55–91.
- Van Soest, L. J. M. 1983a. An easy and reliable method for the rejuvenation of self-incompatible tuber-bearing *Solanum* species. Euphytica 32:601–605.
- Van Soest, L. J. M. 1983b. Evaluation and distribution of important properties in the German-Dutch potato collection. Potato Res. 26:109–121.
- Van Soest, L. J. M., J. G. Hawkes, and W. Hondelmann. 1983a. Potato collecting expedition to Bolivia and the importance of Bolivian germplasm for plant breeding. Z. Pflanzenzücht. 91:154–168.
- Van Soest, L. J. M., H. R. Rumpfenhorst, and C. A. Huijsman. 1983b. Resistance to potato cyst-nematodes in tuber-bearing *Solanum* species and its geographical distribution. Euphytica 32:65–74.
- Van Soest, L. J. M., B. Schöber, and M. F. Tazelaar. 1984. Resistance to *Phytophthora infestans* in tuber-bearing species of *Solanum* and its geographical distribution. Potato Res. 27:393–411.
- Veilleux, R. 1985. Diploid and polyploid gametes in crop plants; mechanisms of formation and utilization in plant breeding. Plant Breed. Rev. 3:253–288.
- Veilleux, R. E., and F. I. Lauer. 1981. Breeding behaviour of yield components and hollowheart in tetraploid-diploid vs. conventionally derived potato hybrids. Euphytica 30:547–561.
- Veilleux, R. E., F. I. Lauer, and S. L. Desborough. 1981. Breeding behaviour for tuber protein in *Solanum tuberosum*-phureja hybrids. Euphytica 30:563–577.
- Vilaró, F. L., R. L. Plaisted, and R. W. Hoopes. 1989. Comparison of cytoplasmic male sterilities in progenies of *Tuberosum* × *Andigena* and *Tuberosum* × *Neo-Tuberosum* crosses. Am. Potato J. 66:13–24.
- Wagenvoort, M. 1988. Chromosomal localization of a recessive gene *tp* controlling the pleiotropic character topiary in *Solanum*. Theor. Appl. Genet. 75:712–716.
- Wagenvoort, M., and M. S. Ramanna. 1979. Identification of the trisomic series in diploid *Solanum tuberosum* L. Group *Tuberosum*. II. Trivalent configurations at pachytene stage. Euphytica 28:633–642.
- Wale, S. J. 1983. The use of micropropagated plants of potato cultivars to determine relative susceptibilities to common scab (*Streptomyces scabies*). Ann. App. Biol. v. 102 Suppl. Tests Agrochem. Cultiv. 4:68–69.
- Wang, P.-J. 1985. Potato tissue culture and its applications in agriculture, p. 503–577. In:

- P. H. Li (ed.), *Potato physiology*. Academic Press, New York.
- Warren, D. S., and J. S. Woodman. 1974. The texture of cooked potatoes: A review. *J. Sci. Food Agr.* 25:129-138.
- Wastie, R. L. 1984. Inoculating plant material by jet injection. *Plant Path.* 33:61-63.
- Wastie, R. L. 1987. The blackleg-soft rot complex, p. 56-72. In: *Potato disease assessment keys*. Eur. Assoc. for Potato Res., Section for Pathology.
- Wastie, R. L., P. D. S. Calagari, H. E. Stewart, and G. R. Mackay. 1988. Assessing the resistance to gangrene of progenies of potato (*Solanum tuberosum* L.) from parents differing in susceptibility. *Potato Res.* 31:355-365.
- Wastie, R. L., and G. R. Mackay. 1985. Breeding for resistance to blackleg: The present and the future, p. 75-77. In: D. C. Graham and M. D. Harrison (eds.), *Rpt. Int. Conf. Potato Blackleg Disease*. Potato Marketing Board and Potato Assoc. of Am.
- Wastie, R. L., G. R. Mackay, P. D. S. Caligari, and H. E. Stewart. 1990. A glasshouse progeny test for resistance to gangrene (*Phoma foveata*). *Potato Res.* 33:131-133.
- Wastie, R. L., and R. M. Solomon. 1988. The contribution and value of resistant cultivars to disease control in potatoes, p. 103-112. In: B. C. Clifford and E. Lester (eds.), *Control of plant diseases: Costs and benefits*. Scientific Publications, Oxford.
- Wastie, R. L., H. E. Stewart, and J. Brown. 1989. Comparative susceptibility of some potato cultivars to dry rot caused by *Fusarium sulphureum* and *F. solani* var. *coeruleum*. *Potato Res.* 32:49-55.
- Weaver, M. L., and H. Timm. 1983. Significance of the fructose/glucose ratio in screening potato breeding lines with processing potential. *Am. Potato J.* 60:329-338.
- Webb, K. J., and C. G. Henshaw. 1982. Morphogenesis in leaflet discs of potato (*Solanum tuberosum* subsp. *tuberosum*), p. 157-158. In: A. Fujiwara (ed.), *Plant tissue culture 1982*. Proc. 5th Int. Cong. Plant Tissue & Cell Culture, 11-16 July 1982. Tokyo, Japan.
- Weller, S. C., J. B. Masiunas, and J. Gressel. 1987. Biotechnologies of obtaining herbicide tolerance in potato, p. 281-297. In: Y. P. S. Bajaj (ed.), *Chap. IV.4., Biotechnology in agriculture and forestry. 3. Potato*. Springer-Verlag, New York.
- Wellving, A. 1976. Studies on the resistance of potato rots caused by *Phoma exigua* var. *foveata* and *Fusarium* species. The Swedish Seed Association, Svalöv, Sweden.
- Wenzel, G., V. A. Bapat, and H. Uhrig. 1983. New strategy to tackle breeding problems of potato, p. 337-349. In: S. K. Sen and K. L. Giles (eds.), *Plant cell culture in crop improvement*. Plenum Press, New York.
- Wenzel, G., and B. Foroughi-Wehr. 1984. Anther culture of *Solanum tuberosum*, p. 293-301. In: I. K. Vasil (ed.), *Cell culture and somatic cell genetics of plants*, Vol. 1. Academic Press, New York.
- Wenzel, G., F. Köler, R. Schuchmann, and B. Foroughi-Wehr. 1984. Selection in vitro for resistances, p. 224-227. In: W. Lange, A. C. Zeven and N. G. Hogenboom (eds.), *Efficiency in plant breeding*. Proc. 10th. Congress, EUCARPIA. Pudoc, Wageningen.
- Wenzler, H. G. Mignery, G. May, and W. Park. 1989. A rapid and efficient transformation method for the production of large numbers of transgenic plants. *Plant Sci.* 63:79-85.
- Wersuhn, G. 1989. Obtaining mutants from cell cultures. *Plant Breed.* 102:1-9.
- Wersuhn, G., K. Kirsch, and R. Gienapp. 1987. Herbicide tolerant regenerates of potato. *Theor. Appl. Genet.* 74:480-482.
- Wheeler, V. A., N. E. Evans, D. Foulger, K. J. Webb, A. Karp, J. Franklin, and S. W. J. Bright. 1985. Shoot formation from explant cultures of fourteen potato cultivars and studies of the cytology and morphology of regenerated plants. *Ann. Bot.* 55:309-320.
- White, J. W. 1983. Pollination of potatoes under natural conditions. *Int. Potato Center Circ.* 11(2):1-2.
- Whitehouse, R. N. H. 1969. An application of canonical analysis to plant breeding. *Genet. Agrar.* 32(Suppl.):61-96.

- Wiersema, H. T. 1972. Breeding for resistance, p. 174–187. In: J. A. de Bokx (ed). Viruses of potatoes and seed-potato production. Pudoc, Wageningen.
- Wiersema, H. T. 1977a. A quick laboratory test for assessing resistance of potato tubers to gangrene (*Phoma exigua* var. *foveata*). *Potato Res.* 20:267 (Abstr.).
- Wiersema, H. T. 1977b. Laboratory testing for the resistance of potato tubers to dry rot (*Fusarium coeruleum*). *Potato Res.* 20:268–269. (Abstr.).
- Wilcox, W. F. 1989. Biological and cultural tests for control of plant diseases. v.4. Am. Phytopathol. Soc. Press, St. Paul, MN.
- Williams, S. B., Jr. 1984. Protection of plant varieties and parts as intellectual property. *Science* 225:18–23.
- Wilson, U. E., S. M. Macken, and M. J. Foxe. 1986. Rapid *in vitro* propagation of virus-indexed potatoes for seed production, p. 249–255. In: L. A. Wither and P. G. Alderson (eds.), *Plant tissue culture and its agricultural applications*. Butterworths, London.
- Winslow, R. D. 1978. An overview of the important nematode pests of potato, p. 16–30. In: *Developments in the control of nematode pests of potato*. Rpt. 2nd Nematode Planning Conf. Int. Potato Center, Lima, Peru.
- Winter, W. 1987. Ermittlung der Bodenverseuchungsstärke und des Krankheitsbefalles der Kartoffelknollen durch Pulverschorf (*Spongospora subterranea* (Wallr.) Lagerh.), p. 83–86. In: *Potato disease assessment keys*. Eur. Assoc. for Potato Res., Section for Pathology.
- Woolfe, J. A. 1987. The potato in the human diet. Cambridge Univ. Press, Cambridge.
- Wooster, P. 1986. Micropropagation of potatoes for variety trials, p. 249–251. In: D. Rudd-Jones and F. A. Langdon (eds.), *Proc. Symp. on Healthy Planting Material*, Univ. Reading, 6–8 Jan. 1986. B. C. P. C. Mono. No. 33. British Crop Protection Council.
- Wooster, P. 1988. Tolerance to virus Y^o. *Aspects Appl. Biol.* 17:103–107.
- Wright, N. S. 1988. Assembly, quality control and use of a potato cultivar collection rendered virus-free by heat therapy and tissue culture. *Am. Potato J.* 65:181–198.
- Wurr, D. C. E. 1982. 'Seed' tuber production and management, p. 327–354. In: P. M. Harris (ed.), *The potato crop: The scientific basis for improvement*. Chapman & Hall, London.
- Yang, M. S., N. O. Espinoza, P. G. Nagpala, J. H. Dodds, F. F. White, K. L. Schnorr, and J. M. Jaynes. 1989. Expression of a synthetic gene for improved protein quality in transformed potato plants. *Plant Sci.* 64:99–111.
- Young, D. A., and H. B. Cannon. 1964. Field plot technique for the estimation of specific gravity of potatoes. *Am. Potato J.* 41:349–356.
- Young, D. A., D. J. Clark, and G. C. C. Tai. 1980. An information storage and retrieval system for potato breeding data. *Am. Potato J.* 57:21–32.
- Zachmann, R. 1973. Untersuchungen über die Variabilität von *Rhizoctonia* im Hinblick auf die Resistenzzüchtung der Kartoffel I. Die Bedeutung der Heterokaryose für die Variabilität des Erregers (Investigations on the variability of *Rhizoctonia* with regard to breeding for resistance in the potato. I. The significance of heterokaryosis to the variability of the pathogen). *Z. Pflanzenkrankh. und Pflanzensch.* 11/12:687–703.
- Zadina, J. 1971. Vyber vynosnych krizencu brambor podle vynosu sklizne semenacu (Selecting highly productive potato crosses according to the performance of seedlings). *Genetika A Slechteni* 7:269–273.
- Zadina, J. 1979. Extreme resistance of potatoes to virus S and procedures for its breeding utilization. *Scientia Agr. Bohemoslovaca* 11:157–168.
- Zafar, M. A. 1955. Application of certain hormones to prevent flower abscission in two potato (*Solanum tuberosum*) varieties. *Am. Potato J.* 32:283–292.
- Zielke, R., and K. Naumann. 1987. Ein Beitrag zur Resistenzprüfung bei Kartoffeln gegen den Erreger der Bakterienfäule, *Corynebacterium sepedonicum* (Spieckermann and Kotthoff) Skaptason and Burkholder, anhand ausgewählter DDR-Sorten und Stämme

- (Testing of selected GDR-potato varieties for resistance to the pathogen of bacterial ring rot, *Corynebacterium sepedonicum* (Spieckermann and Kotthoff) Skaptason and Burkholder). *Archiv Züchtungsforschung* 17:145-161.
- Zink, R. T., and G. A. Secor. 1982. Interaction of fungal wilt pathogens and potato blackleg. *Plant Dis.* 66:1053-1056.
- Zitnak, A., and M. A. Filadelfi. 1985. Estimation of taste threshold of three potato glycoalkaloids. *Can. Inst. Food Sci. Technol. J.* 18:337-339.
- Zitnak, A., and G. R. Johnston. 1970. Glycoalkaloid content of B5141-6 potatoes. *Am. Potato J.* 47:256-260.
- Zott, A., and C. Janke. 1983. Interactions between *Phoma exigua* var. *foveata* (Foister) Boerema and other potato dry rot pathogens. *Arch. Phytopathol. Pflanzenschutz.* 19:15-28.
- Zrust, J. 1983. Rychlost fotosyntézy různých genotypu bramborů. *Rostlinna Vyroba* 29:563-576.
- Zrust, J., and A. Smolikova. 1977. Rozdíly v rychlosti fotosyntézy u Krizencu a některých rodičovských odrůd brambor (Differences in the rate of photosynthesis for crosses and some parental cultivars of potatoes). *Rostlinna Vyroba* 23:723-732.