A dominant major gene for hypersensitivity (*Nm;* Ross & JACOBSEN 1976) was found in *S. megistacrolobum* EBS 1787. It is perhaps more advantageous to use a provenience of *S. gourlayi* instead. This line, as well as its ssp. *tuberosum* hybrids, shows a remarkably high infection resistance, being effective even when graft-inoculated (DZIEWOŃSKA & OSTROWSKA 1978). The reaction is inherited by one dominant major gene *(Gm)* in cooperation with another gene that intensifies the reaction (WÁS & DZIEWOŃSKA 1984). BAGNALL (1972) found *S. polytrichon* and *S. microdontum* to be resistant.

7.2.5 Virus S (PVS)

PVS and PVM are closely related. They often cannot be distinguished by means of indicator plants. A successful diagnosis is possible by ELISA serology with monoclonal antibodies (Section 10). The yield reduction caused by this virus is relatively low, seldom reaching 15 %. Transmission occurs through wound contact and, with some strains, additionally by aphids (BODE & WEIDEMANN 1971, KOSTIV 1981). The symptoms are almost invisible. Recognizing and roguing of diseased plants is therefore difficult and up to 1950 very many cvs. were latently infected with PVS, some even totally. Thereafter production of PVS-free seed potatoes was started by means of meristem culture (Section 10).

Differences in resistance to infection with the spray gun were studied by HUNNIUS (1969 b). The cv. Adretta (German Democratic Republic) is very resistant (ULRICH & MÖLLER 1977). The US-cv. Saco is completely protected against infection in the field by an intensive expression of the type of infection resistance. BAERECKE (1967 b) assumes a recessive inheritance conditioned by minor genes. BAGNALL & YOUNG (1972) held one recessive major gene responsible.

A type of localized hypersensitivity is represented in a Bolivian cv. of ssp. *andigena* (P. I. 258 907) and inherited by one dominant major gene (BAERECKE 1967 a, ZADINA 1977 b, MAKAROV 1975). For selection purposes the same methods as for PVY are applied (WÁS & DZIEWOŃSKA 1984). The cv. 258 907 is relatively susceptible to PLRV and PVY. Therefore, it is recommended to choose a resistant parent in crossings. The first cvs. with the gene *Ns* were bred by SARVARY in Hungary (Szignal) and by WRIEDT in the FRG (Fantasia).

7.2.6 Virus A (veinal mosaic virus, PVA)

PVA, as a member of the potyvirus group, is closely related to PVY in its biochemical characteristics. The symptoms, however, are different and restricted to a coarse mosaic or mottle. Its distribution is rather sporadic and it does not offer problems to the breeder because the majority of cvs. carry the gene Na for localized hypersensitivity (Ross 1958 b, COCKERHAM 1970, see also STEGEMANN & SCHNICK 1985). The presence of this gene is assessed by grafting onto an PVA-infected potato stock. The necrotic reaction often is visible on the very young buds at the scion apex only. The gene Ry_{sto} for extreme resistance to PVY is also active against PVA.

7.2.7 Tobacco rattle virus (stem mottle virus, spraing, TRV)

Certain strains of this virus cause a coarse mottle of darker and mostly greater light green patches on the leaves. The symptoms are to be seen on some of the stems only. Often, particularly in certain host species, only the roots are infected. Tubers can be misshapen and necrotic arcs of a few mm may appear in the tuber flesh. With some strains irregular spheres of 1–2 cm diameter are formed with a necrotic outer layer. They appear as necrotic rings on the surface of the tuber. The symptoms are similar to those of the mop-top virus (BEEMSTER & ROZENDAAL 1972, VAN HOOF 1972) occurring occasionally in the U. K. and to a physiological disorder called Eisenfleckigkeit (WEIDEMANN 1981). The detection of TRV in tubers was improved recently by application of the complementary (c) DNA method (HARRISON et al. 1983; Section 10).

The populations of TRV are composed of strains of different severity. Some prefer the sprouts for propagation, and others the tubers. The latter strains seldom migrate to the

Aardevo Exhibit 1013
Page 0075

sprouts. The virus is transmitted by several species of the eelworm genera *Trichodorus* and *Paratrichodorus*. These are distributed mainly in sandy soils. Most infections seem to result from new inoculations and not from tuber transmission.

Selection is performed by natural infection in trials on nematode- and TRV-infested fields. Several replications over a number of years are necessary to gain reliable results. Several variety lists inform about resistant cvs.

Cv. Stormont Enterprise fails to show symptoms. About 50 % of its progeny with a susceptible parent remained symptomless (JELLIS & GRAY 1980). The authors conclude on a monomer-dominant inheritance with involvement of minor genes. WIERSEMA (1972) assumes that the necrotic response, often observed with TRV, indicates a tendency for hypersensitivity similar to the intolerance in the case of PLRV.

7.2.8 Spindle tuber viroid (PSTV)

Viroids are extremely small circular one-stranded infectious RNA molecules of low molecular weight and viruslike characteristics, but not associated with protein. They presumably originated from nuclear genes in the course of evolution (DIENER 1979). Symptoms are missing in many cases. In others the tubers are elongated, and in some cvs. leaves and tubers can be ± deformed (PFANNENSTIEL & SLACK 1980). Plants from diseased tubers are often healthy (CHRZANOWSKA & KOWALSKA 1981). The viroid represents a danger, important not only because of its effect on tuber yield and form but also because it is transmitted through the true seed in addition to transmission by wound contact and insects. Its spread among crossing parents would be a severe burden for variety breeding work. Particular caution has to be taken when true seed is sent abroad.

Scopolia sinensis and the tomato cv. Rutgers are used as indicator plants. They react with necrosis of the veins. Weak strains often escape detection. SINGH (1984) recommends *S. berthaultii* as a reliable indicator plant. Biochemical diagnosis is possible with polyacrylamidgelelectrophoresis and cDNA technique (Section 10). PFANNENSTIEL et al. (1980) found 20 % potato plants infected one month, and 70 % two months after inoculation. All tubers grown from infected plants in these trials reacted positively.

No cv. could be found reacting with hypersensitivity or extreme resistance. A Polish cv. remained free of symptoms even after recapitulated sap inoculation (CHRZANOWSKA & KOWALSKA 1981). BAGNALL (1972) inoculated many wild species. Only *S. guerreroense* turned out to be free from PSTV in back tests. SALAZAR (1981) could not infect *S. acaule* Och 11603.

7.3 Potato cyst eelworm, *Globodera rostochiensis* (Woll.) Behrens and *G. pallida* (Stone) Behrens

Combining resistance against the potato cyst eelworm to the genomes of cvs. is one of the most prominent goals in potato breeding. It is characteristic that since some years Dutch and German potato breeders have been taking an eelworm resistant parent for every cross they make.

The two cyst-forming nematode species of the genus *Globodera*, parasitizing the potato, are distinguished by some morphological traits, and, above all, by the colour of their cysts. While those of *G. rostochiensis (G. r.)* pass through a phase of golden colour for some weeks, those of *G. pallida (G. p.)* remain white or pale yellow until shortly before they drop off.

G. r. is the main species in infested fields in Great Britain, Belgium, France, the Federal Republic of Germany, the German Democratic Republic, the Netherlands and Southern Scandinavia. *G. p.* is sporadically intermixed. Most of the populations belong to the pathotype Pa-3. Nematode infested fields in some parts of Germany contain mixtures of *G. r.* and *G. p.* A higher percentage of *G. p.* is observed in the northern parts close to the

Aardevo Exhibit 1013
Page 0076

border with the Netherlands. In Great Britain many infested fields are contaminated with *G. p.* In the Netherlands, the contamination is less.

The life cycle starts with the development of larvae in response to hatching substances excreted by the roots of host plants. Other compounds attract the larvae to the roots which become invaded. The larvae differentiate into sexes. The females, being larger, need more feeding than the males. The cellwalls around the eelworm are dissolved and a large syncytium is formed, supplying the eelworm with food. After copulation, the females penetrate through the root surface and develop into the egg-containing cysts. The cysts remain attached to the roots and, partly, to the tubers for about four weeks before they drop off. A cyst contains 200–300 eggs, some of which have already developed to small larvae. Each year only a certain number of eggs hatches. The cysts can survive about 8–10 years in the soil. When no hosts are grown or the field is laid fallow a decline of 40 % in the cyst population is generally accepted. Crop on an infested field must cause at least the same decline if the respective cv. is acknowledged as resistant. In pot trials a susceptible cv. enhances the infestation 2 to 16-fold according to the genotype and environment, but also depending on the aggressivity of the population (*Tab. 13;* STONE et al. 1979).

Routine selection tests for resistance are performed in the greenhouse. Small tubers, or tuber eyes, are placed in a pot of 6–8 cm diameter or in bio-test containers (BEHRINGER 1967). Tests with seedlings must be interpreted with caution, because fewer cysts are formed as compared with tuber born plants (GONZALEZ & SCURRAH 1983, PHILLIPS 1984). The pots must always be filled with the same kind of soil mixture. 30 cysts or their content are added in small nylon sacks (Pi). The newly formed cysts are isolated by application of Fenwick water and alcohol or aceton flotation method, and counted (Pf). In the case of H_1-genotypes five replications and the counting of cysts visible at the outside of the rootball is sufficient, while in other cases, seven replications are recommended as well as counting of total cysts or even of eggs and larvae (KORT et al. 1972, FORREST & HOLLIDAY 1979). PHILLIPS et al. (1980) used closed plastic containers planted with tubers and placed in darkness. The correlation between cysts outside on the rootball and those newly formed in the entire pot is strong only with Ro-5 and in the presence of H_1. For tests with G. p. see Anon. (1983 c). PHILLIPS (1981) and DALE & PHILLIPS (1982), in order to assess roughly the value of a progeny, plant 20 seedlings together in a pot and count the cysts outside on the rootball. This test can be applied only when the presence of major genes in the population is excluded. MUGNIERY

Tab. 13: Reaction of different eelworm populations of some pathotypes found in the Federal Republic of Germany and adjacent countries with the differentials of the International Scheme. Number of total newly formed cysts (Pf)

Reaktion verschiedener Nematodenpopulationen einiger Pathotypen aus der Bundesrepublik Deutschland und angrenzenden Ländern mit den Differentialklonen des Internationalen Schemas (RUMPENHORST, pers. comm.)

	pathotypes – *Pathotypen*								
	Pa-1	Pa-2				Pa-3			
populations *Populationen*	1	2	3	4	5	6	7	8	9
Pi	40	20	25	25	25	20	25	30	33
ssp. *andigena*	1033	761	507	1106	898	1009	1241	635	757
KTT 60-21-19	1216	673	850	974	446	1604	1260	932	497
VT^n 58.1642/4	540	138	499	420	304	1142	1149	288	338
VT^n 62.33.3	22	1	20	7	59	90	75	380	205
VT^n 65.346/19	22	13	15	25	44	134	457	–	480
P 55/7	32	138	164	–	59	185	–	418	–

Aardevo Exhibit 1013
Page 0077

(1983) introduced the Petri dish technique. The roots of small tuber-eye pieces are inoculated by placing 3–5 freshly hatched larvae directly on the roots. 30 days later adult females protruding from the roots can be observed and counted. This method is refined by using a photograph of 16 predetermined grids of the root tray to count the females and cysts (Anon. 1984 a).

As with other pathosystems, a non-necrogenic resistance can be distinguished from a necrogenic one. The non-necrogenic resistance becomes evident when susceptible cvs. differ in the numbers of cysts they form (DALE & PHILLIPS 1985). This resistance presumably belongs to the type of field resistance. It is composed of single components differing in the cvs. in their effectivity, such as formation of the hatching substance (DESHMUK & WEISCHER 1970, FORREST & PHILLIPS 1984) sex differentiation and perhaps other traits. This needs more elucidation. The non-necrogenic reduction, because of being unsatisfactory, is not of direct benefit for the crop. However, when a hypersensitive parent in a cross is supplemented by a field resistant one the resistance of the progeny is raised remarkably.

The necrogenic resistance (hypersensitivity) is characterized by a necrogenic degeneration of the syncytium (GIEBEL 1982). The female larvae especially suffer then from insufficient feeding. They die off or remain small, containing fewer eggs. Only genotypes with a Pf/Pi-value of $\leqq 1$ lead to a decline in the number of cysts. According to an international regulation, only those cvs. with a Pf/Pi-value (multiplication rate) of $\leqq 0.6$ (KORT et al. 1977) are recognized as resistant and are allowed to be grown in contaminated fields. This means a decontamination of 40 % (see above). It should be noted here that cvs. with a Pf/Pi-value between 0.6 and 2 or more (against 20, 30 and more in the case of susceptible cvs.) are able to suppress a rapid contamination in fields containing only single cysts. Breeding products with Pf/Pi 0.6–2, are allocated today to the group of susceptibles. Such cultivars were better officially recognized as moderately resistant and grown and admitted on uncontaminated fields or fields with only single cysts.

Tolerance, although not a resistance type in the proper sense, has nontheless a meaning in breeding for resistance to nematodes. The invading and feeding larvae damage a resistant crop despite the crop's hypersensitive reaction and lead to a certain yield reduction (STELTER & MEINL 1980, HUIJSMAN 1983). Tolerance should therefore not be neglected in breeding for eelworm resistance.

It should be noted that the growth of a resistant cv. does not eradicate all eggs and cysts in the soil. The same is true for the chemical decontamination, especially in the case of *G. p.* A combined treatment with resistant cultivars supplemented by nematicides is necessary.

Both *Globodera* species exist with several pathotypes. The field populations can be divided into five pathotypes of *G. r.* and three of *G. p.* by means of seven differentials (KORT et al. 1977; *Tab. 14*). These represent breeding lines that are back-cross hybrids, one with ssp. *andigena* CPC 1673 and others with *S. kurtzianum, S. multidissectum* and *S. vernei.* The multiplication rates for resistance in single experiments vary between 0 and 1.7 with 0.6 on the average. FULLER et al. (1977) and STONE et al. (1979) extended the scheme by introducing the hybrid D 47/11 (ssp. *andigena* CPC 1673 × *S. multidissectum* × ssp. *tuberosum*) as an additional differential. By this it was possible to distinguish a further pathotype of *G. p.* (Pa-4). Using most of the differentials of the International Scheme, CANTO & SCURRAH (1977) set up schemes with other denominations of the pathotypes. Ro-1 is in the Andean Schema R_1A, Pa-2 = P_4A and Pa-3 = P_5A. Several new pathotypes were detected in the Andes. Moreover, both species, and perhaps the pathotypes too, can be differentiated by means of one- or two-dimensional electrophoreses of their cyst proteins. This would make identification easier (TRUDGILL & CARPENTER 1971, STEGEMANN et al. 1982). The following populations known from experimental work in the literature could be classified (RUMPENHORST & Ross, unpubl.): Hohenried = Ro-1, Pont = Ro-2, Husberg = Ro-4, Wiesenthal = Pa-1, Winsen, Nilgiris (Indien), Neuseeland, Huancayo (= Chocón, Peru) and SCHWÖRSHEIM = Pa-2, Rehenbühl, Oberlangen, Pustertal, Innsbruck and Otusco (= Agallpampa, Peru) = Pa-3.

Aardevo Exhibit 1013
Page 0078

Tab. 14: International scheme for the classification of populations of *Globodera rostochiensis* and *G. pallida*
Internationales Schema zur Einteilung von Populationen von Globodera rostochiensis und G. pallida (KORT et al. 1977)

Differential-klone	Resistenz-code	1	2	3	4	5	6	7	8	9
		national denomination *nationale Bezeichnung*	British A Dutch A Hiltrup	Dutch B Oberstein-bach	Dutch C	Dutch F	Harmerz	British B	Dutch D	Frenswegen Chavorney Dutch E British E
		internat. Pathotypen	Ro1	Ro2	Ro3	Ro4	Ro5	Pa1	Pa2	Pa3
susceptible cv. *anfäll. Sorte*			+	+	+	+	+	+	+	+
cv.-Sorte ex ssp. *andigena* CPC 1673	Ro 1, 4		−	+	+	−	+	+	+	+
S. kurtzianum-hybrid 60.21.19	Ro 1, 2		−	−	+	+	+	+	+	+
S. vernei-hybrid GLKS 58.1642/4	Ro 1, 2, 3		−	−	−	+	+	+	+	+
S. vernei-hybrid 62.33.3	Ro 1, 2, 3, 4		−	−	−	−	±	−	−	+
S. vernei-hybrid MPI 65.346/19	Ro 1, 2, 3, 4, 5		−	−	−	−	−	+	+	+
S. multidissectum-hybrid P 55/7	Pa 1		+	+	+	+	+	−	+	+

In the case of *G. r.*-populations the classification is easy. The differentiation among *G. p.*-pathotypes is mainly based on the *S. vernei*-back-crosses hybrid 62.33.33 (KORT et al. 1972, 1977). The response of this clone to different eelworm populations is not clear-cut and not comparable with the other differentials *(Tab. 13)*. The Pf/Pi-value of some field populations occasionally covers a range between 0.6 and 1.0, making it difficult to decide whether the population belongs to Pa-2 or Pa-3 or whether it is a mixture (see also STONE et al. 1979). STOREY & MARKS (1983) obtained a more precise and faster determination of the multiplication rate by measuring the adenosintriphosphate content of the Pi- and Pf-cysts by bioluminescent photometry.

The continuous growth of a Ro-1-resistant cv. on fields infested with mixtures of Ro-1 and Pa-pathotypes causes a shift in the composition of the mixture (JONES 1980). The assumed existance of a gene-for-gene system (Section 7.6) has become the subject of controversy (TURNER et al. 1983, CALIGARI & PHILLIPS 1984). It seems difficult to establish such a system when, as in the case of eelworm resistance, minor genes are varying strongly the effects of major genes. The establishment of new pathotypes does not seem serious in the light of practice, since application of nematicides, crop rotation and the relatively restricted spreading of the worms as compared with fungi militates against such a development as being a fast one.

The basis for breeding is the necrogenic resistance or hypersensitivity. Hypersensitively responding, cyst number reducing genotypes are not rare among ssp. *andigena* cvs. and wild species. They mainly carry one dominant major gene of different expressivity in the different sources, accompanied by a minor gene complex that helps to complete the resistance. During the several necessary back-crosses, the minor gene complex is dissolved. After several back-cross generations a residual resistance remains. This is always lower that it was in the ssp. *andigena* or in the wild species, except when the gene H_1 is present. The resistance can be improved by addition of minor genes from the original or another resistance source or provided by »susceptible« parents possessing field resistance.

Aardevo Exhibit 1013
Page 0079

The first screening performed by MAI & PETERSON (1952) and – at the Commonwealth Potato Collection – by ELLENBY (1948, 1954) brought to light the very high resistance of five accessions of ssp. *andigena* (CPC 1673 etc.) and of an accession of *S. vernei* (syn. *S. ballsii*). Ssp. *andigena* CPC 1673 (gene H_1), *S. vernei* and later on *S. spegazzinii* (gene *Fb*) were taken into breeding work and conveyed resistance to many cvs. *(Tab. 15)*. It must be regarded as an impressive success in potato breeding that today more than 60 cvs. in the Federal Republic of Germany contain the gene H_1. These cvs. cover more than 40 % of the seed potato area. The H_1-cv. Granola was the most grown cv. in Germany in 1980 and the H_1-cv. Maris Piper, bred by *Howard* and coworkers, the most widely spread in Great Britain. Two other valuable traits characterize CPC 1673: the gene Rx_{adg} giving complete protection against PVX and a heterotic potency shown when combined with ssp. *tuberosum*. *The gene* H_1 was detected by HUIJSMAN (1955) and TOXOPEUS & HUIJSMAN (1953) and has the highest expressivity among the major genes for eelworm resistance so far known. It is located distantly from the centromere (TELLHEIM et al. 1982). The gene is brought into action only by the pathotypes Ro-1 and Ro-4 *(Tab. 14)* and causes a reduction of the newly formed cysts very often to about zero (KORT et al. 1977). This high resistance is maintained in the course of back-cross-breeding. HOWARD et al. (1970) found a similarly acting gene in ssp. *andigena* CPC 1690. It has been transmitted to the cv. Maris Anchor. The single H_1-cvs. nevertheless differ considerably in their decontamination effect. The Pf/Pi-values vary between 0.01 and 1.31 (HEINICKE 1984).

As outlined above, by far the majority of eelworm resistant cvs. are resistant only to Ro-1 and Ro-4. The demand for cvs. resistant to other pathotypes has led to the introduction of further cvs. of ssp. *andigena* and of *S. vernei* and *S. spegazzinii* into breeding. Both wild species are resistant to perhaps all pathotypes of *G. r.* and *G. p.* (Ross & HUIJSMAN 1969). HOWARD & FULLER (1971) found the cv. CPC 2802 of ssp. *andigena* to confer resistance to Pa-1 and Pa-3. The resistance was first considered monomeric (gene H_3), but later on a polygenic resistance was assumed (PHILLIPS & DALE 1982). LANDEO et al. (1976) found a dominant gene for resistance to at least the population Otusco of Pa-3. GONZALEZ & SCURRAH (1982) observed a Bolivian clone of ssp. *andigena* with a multiplication rate of 0.5 when screened with Pa-2 ($= P_4A$). Breeding with these accessions of ssp. *andigena* has not resulted in a cv. so far.

Before crossing, the diploid wild species were brought to the tetraploid level with colchicine. Part of the resistance faded away, as described above, during the necessary back-cross generations.

Several major genes are assumed to be responsible for the resistance of *S. vernei*-hybrids to *G. r.* PLAISTED et al. (1962 a) found two genes, *B* and *C,* for resistance to Ro-1. One of these seems identical with H_1, the other, whilst acting similarly, is situated at a different locus (SCURRAH et al. 1973).

The genetics of the resistance of *S. vernei* to *G. p.*-pathotypes are still a matter of discussion (ROTHACKER & STELTER 1957, Ross & HUIJSMAN 1969, HUIJSMAN & LAMBERTS 1970, HOWARD & FULLER 1975, KORT et al. 1972, 1977, FULLER & HOWARD 1977, FORREST & HOLLIDAY 1979, DALE & PHILLIPS 1982, TURNER et al. 1983, UHRIG & WENZEL 1981). A 1 : 1 segregation can be recognized in some progenies when the limit between the resistant class and the susceptible one is stated by Pf/Pi = > 1.0. A stronger reduction of cyst formation to an agronomically valuable number seems only to occur when the seedlings in question carry additional supporting minor genes or a major one from another source. It is, therefore, recommended that another resistant partner be combined with the *S. vernei*-back-cross parent. In particular, a resistance to Ro-4 is difficult to reach when H_1 is absent.

Different *S. vernei* accessions have been attributed to the eelworm resistance of to date 35 cvs. in the Netherlands, the Federal Republic of Germany, Denmark and Breat Britain *(Tab. 15)*. ROTHACKER & STELTER (1957) and ROTHACKER (1959) started breeding with colchicine doubled derivative of *S. vernei* in the Institut für Kartoffelforschung Gross Lüsewitz (German Democratic Republic). Back-cross lines with ssp. *tuberosum* (VT^4 resp.

Aardevo Exhibit 1013
Page 0080

Tab. 15: Eelworm resistant cvs. with *S. spegazzinii (spg), S. vernei (vrn)* and additional ssp. *andigena* CPC 1673 *(adg)* in their pedigree and the presence of the gene Rx_{acl} or another major gene for hypersensitivity or extreme resistance to PVX (see Section 7.2.3)

Nematodenresistente Sorten mit S. spegazzinii (spg), S. verneï (vrn) und zusätzlich ssp. andigena CPC 1673 (adg) in ihrer Abstammung und die Gegenwart des Hauptgens Rx_{acl} oder anderer Hauptgene für Überempfindlichkeit oder extremer Resistenz gegen PVX

cultivars *Sorten*	country *Land*	sources of eelworm resistance *Herkunft der Nematodenresistenz*			resistant to pathotypes *resistent gegen die Pathotypen*								resistant to PVX *resistent gegen PVX*
					Ro 1	2	3	4	5	Pa 2	3		
Amalfy	NL	*adg*		*vrn* I	r	r	r	r	r				
Amera	NL	*adg*		*vrn* I	r	r	r						
Amethyst	NL			*vrn* I	r								
Assia	D	*adg*		*vrn* I	r				r				Rx_{acl}
Astarte	NL			*vrn* I	r								[2]
Atrela	NL	*adg*		*vrn* I	r	r	r			r			[2]
Aula	D	*adg*		*vrn* II	r								
Barbara[1]	D	*adg*	*spg*	*vrn* I	r	r	r	r	r				Rx_{acl}
Compagnon	F, NL	*adg*		*vrn* I	r			r					
Cordia[1]	D	*adg?*	*spg*		r				r				
Culpa	D	*adg*		*vrn* II	r								
Danva	DK	*adg*		*vrn* I	r		r	r		r	r		
Darwina	NL	*adg*		*vrn* I	r	r	r			r			[2]
Elkana	NL	*adg*		*vrn* I	r	r	r						
Esta[1]	D	*adg*	*spg*		r				r				
Fecuva	DK	*adg*		*vrn* I	r			r					
Fiesta	D	*adg*		*vrn* II	r								
Fiona	UK			*vrn* III									
Fox	D			*vrn* I	r	r	r		r				
Franzi[1]	D	*adg*	*spg*		r	r	r	r	r				
Hanne	D	*adg?*	*spg*		r								
Heidrun[1]	D		*spg*		r				r				
Hilta	D		*spg*		r	r	r		r				
Hydra	D	*adg*		*vrn* II	r								
Krostar	NL			*vrn* I	r								
Mara	NL	*adg*		*vrn* I	r	r	r						
Miranda	D		*spg*		r	r	r	r	r				
Nausica	NL			*vrn* II	r								
Nordlicht	D	*adg*		*vrn* I	r								
Pansta	NL	*adg*		*vrn* I	r	r	r			r			[2]
Ponto	D		*spg*		r	r	r	r	r				
Produzent	NL	*adg*		*vrn* I	r	r	r			±r			[2]
Promesse	NL	*adg*		*vrn* I	r	r	r			r			[2]
Proton	NL	*adg*		*vrn* I	r	r	r			r			[2]
Pruceras	NL, D			*vrn* I	r	r	r						
Puntila	D	*adg*		*vrn* II	r								
Roeslau[1]	D			*vrn* I	r		r		r				Rx_{acl}
Ronea	D		*spg*		r								
Roxy	D	*adg*		*vrn* II	r								
Santé[1]	NL	*adg*		*vrn* I	r	r	r			r			[2]
Senator	NL			*vrn* I	r								[2]
Ute[1]	D			*vrn* I	r	r	r		r				Rx_{acl}
Veenster	NL	*adg*		*vrn* I	r	r	r						[2]
Wega[1]	D		*spg*		r				r				

[1] carrier of the gene Ry_{sto} for extreme resistance to PVY ex *S. stoloniferum*
Sorte besitzt das Gen Ry_{sto} für extreme Resistenz gegen PVY

[2] *carrier of a gene for hypersensitivity or extreme resistance to PVX*
Sorte besitzt ein Gen für Überempfindlichkeit oder extreme Resistenz gegen PVX

Cvs. with supply of eelworm resistance only from ssp. *andigena* CPC 1673 are not enlisted here
Sorten mit Nematodenresistenz, die nur von ssp. andigena CPC 1673 stammt, sind nicht aufgeführt
Vrn I, II, and III see text

Aardevo Exhibit 1013
Page 0081

VT^5) were sent to other European institutes by way of exchange. One of these hybrids (GLKS 58.1642/4) became the Dutch line 22.731. Another GLKS-hybrid (VT^2) was crossed as male with *S. vernei* CPC 2787 × *S. vernei* CPC 2488 × T^n. The well-known hybrids 62-33-3 originated from this cross, according to HOWARD (pers. comm.). 62-33-3 and the hybrid MPI 65.346/19 (hybrid of a Gross Lüsewitz VT^n-line combined with MPI 55.957/54) became differentials of the International Scheme. The hybrid 62.33.3 and its further back-cross generations gave rise to most of the Dutch cvs. with genes of *S. vernei* (*Tab. 15, vrn* I; KORT et al. 1972, 1977, Anon. 1981 a). The MPI hybrid 65.346/19, carrying in addition the genes *Rx* and *Ry,* was included in the parentage of some German cvs. Another *S. vernei* accession (EBS 218/16) was collected by H. BRÜCHER (*vrn* II), while the cv. Fiona (*vrn* III) is bred with *S. vernei* CPC 2488 × CPC 2487 (GLENDINNING, pers. comm.).

S. spegazzinii (syn. *S. famatinae*) is the third species which contributed genes for resistance to a number of cvs. *(Tab. 15).* Three major genes could be identified (Ross 1962, MOMENI et al. 1969, BOUWMAN & Ross 1972, Ross et al. 1974, HUNNIUS & SCHEIDT 1974). *Fa,* conferring resistance to Ro-1 and Ro-2 but not to Ro-5, *Fb* to Ro-1 as far as Ro-5, and *Fc* to some pathotypes of both *G.* species. Breeding was performed through four to six back-crosses with the gene *Fb.* Higher back-cross hybrids forming 0–2 cysts deliver progenies with on average fewer cysts than those parents with 3–5 and more cysts. As in the case of *S. vernei*-hybrids here, too, the combination with alien genes (H_1 a. o.) enhances the resistance. Minor genes can vary the resistance to both sides. The effect of Fb on other pathotypes than Ro-1 is present but less intensive. Among the nine cvs. with the gene Fb, only cvs. Franzi and Miranda possess an agronomic resistance to all pathotypes of *G. r. (Tab. 15).*

Whilst the problems in breeding cvs. with resistance to *G. rostochiensis* have been solved, resistance to *G. pallida* still offers difficulties because only very few seedlings with satisfactory resistance result from the crosses, and their resistance does not cover as many pathotypes as required. Several new strategies can be adopted.

They are result of the theoretical consideration of the complementary action of different components for resistance and of the experiences discussed above (see also SCURRAH & FRANCO 1983, and *Tab. 15*). The genetic constitution, based on either major or minor genes or on both together, does not act against one main pathotype only but against others as well, albeit to a lesser degree. Therefore, a combination breeding »within« eelworm resistance must be performed first of all. That means that both parents of a cross must present at least a certain resistance level and both should originate from different sources.

One such approach involves interdihaploids of the constitution (dihaploid × wild species) × $dihaploid^n$. The wild species were *S. gourlayi, S. oplocense, S. sparsipilum, S. spegazzinii* and *S. vernei* (LANGTON & Ross 1982, Ross unpubl.). After upgrading, the interdihaploids were crossed with eelworm resistant tetraploids. Diplogametic tetraploids resulted with a remarkable level of resistance to *G. pallida* and *G. rostochiensis* and have been distributed to breeders (UHRIG 1983).

A further approach follows the analytic-synthetic breeding scheme (Section 5.1.4). It starts with resistant monohaploids obtained by androgenesis from the above mentioned dihaploid S. gourlayi- and S. vernei-hybrids (WENZEL & UHRIG 1981, UHRIG & WENZEL 1981, UHRIG 1982, 1983) and involves pre-breeding at the diploid level (Section 5.1.2.3). About 20 % of the plants spontaneously doubled up to diploids and revealed equal or higher Pa-3 resistance compared with the parents. According to DE, MAINE (1982, 1984 a) part of the dihaploid offspring possesses higher resistance than the tetraploid parent (*S. vernei* back-cross hybrid). Otherwise, the return to the tetraploid level can be accomplished through 4x-2x-crosses (Ross & JACOBSEN 1976, DE, MAINE 1982) as well as by means of colchicine. In the latter case, it was observed that the resistance of some tetraploid duplex hybrids of *S. gourlayi, S. sparsipilum* and *S. vernei* with ssp. *tuberosum* was either equal or reduced (LANGTON & Ross 1982). The multiplex condition seems not or nearly not to affect the expressivity of the genes for resistance.

Aardevo Exhibit 1013
Page 0082

Another solution would be to detect and utilize further wild species with outstanding resistance. New introductions from the Brunswick genebank were tested with 4 Ro- and 3 Pa-pathotypes. Differentiation was made, as a pre-screening, between resistant (0–5 cysts at the rootball surface), moderately resistant (6–15 cysts) and susceptible types (VAN SOEST et al. 1983 b). FRANCO & MATOS (1983) in Lima tested 215 accessions of the genebank of the International Potato Center at Lima comprising 61 wild species with Pa-2 and Pa-3, for three years and found as best sources for resistance: *S. lignicaule* with Pf/Pi = 0.63 and 0.21, *S. megistacrolobum* (0.58 and 0.68), *S. sparsipilum* (0.65 and 0.40) and *S. vernei* (0.62 and 0.39). For previous screening results see VAN SOEST & SEIDEWITZ (1981).

Whether in the course of back-crosses the high resistance of these wild species will remain maintained better than in the case of those already used in breeding, cannot be foreseen.

Moreover, very resistant or even non-host species exist at the border of the host range of *Globodera.* These are sexually incompatible with *S. tuberosum,* e. g. *S. suaveolens* (GOFFART & Ross 1954), tobacco cvs., *Physalis philadelphica, Petunia* etc. (SEMBDNER 1964). As a prospect to the future it should be mentioned that these species are candidates for asymmetric somatic fusions (Section 5.2.3). Somaclonal variation is also observed with eelworm resistance (MACKAY 1984).

7.4 Late blight, *Phytophthora infestans* (Mont.) de Bary

Phytophthora infestans, causing haulm destruction and decay of the tubers, is the most important fungal parasite of the potato. Its importance has become ever greater since potato cultivation spread to countries with warm and humid climates. There it is a prime production constraint.

Two types of resistance are encountered: hypersensitivity (vertical or specific resistance) and field resistance (horizontal or general resistance, VAN DER PLANK 1968). Hypersensitive genotypes are characterized by a necrotic response of the inoculated cells and those close to them. The hypersensitivity is conditioned by a series of very expressive major genes, each of which brought into action by distinct pathotypes. The field resistance is a complex of different components resulting in the hindrance of the parasitic attack on the host, and is inherited by minor gene effects. Both types of resistance occur jointly in wild species like *S. demissum, S. bulbocastanum, S. polyadenium, S. stoloniferum, S. vernei, S. verrucosum* and others (TOXOPEUS 1964, GRAHAM 1963, BLACK 1970) while unhybridized pure S. tuberosum-ovs. carry minor genes for field resistance of different degrees only.

During the first centuries after introduction of the potato from South America to Europe and North America, *P. i.* was not a harmful parasite. This changed after the adaptation of the parasite to the climatic conditions of the Northern hemisphere. The first heavy attack of the fungus happened in the middle of the 19th century (Irish famine, BURTON 1966). Other *P. i.*-epiphytotics in the next decades caused a heavy turnover of the cvs. assortment. It seemed a solution when SALAMAN and others since about 1910 introduced *S. demissum* into breeding (Section 2.5). This species by means of its major genes for hypersensitivity conveyed complete protection to the back-cross hybrids *S. demissum* × ssp. *tuberosum* in the breedings gardens, but only in the first years of their existance.

The fungus, after being confronted with major genes for hypersensitivity in the new hybrid breeding lines, started to form pathotypes. The first heavier infections were observed about 1932. Different pathotypes infecting different hybrid breeding lines could be made out. Detailed investigations allowed the setting-up of an international gene-for-gene scheme (BLACK et al. 1953) whereby dominant host genes were matched by corresponding genes for virulence of the parasite *(Tab. 16).* New recessive genes will be developed by the pathogen in the course of selection pressure of host genes. The genotype R_1 was infected by the simple pathotype 1, by the complex pathotypes 1.2, 1.3, 1.2.3 and so on, but not by 2, 2.3, 3.4 etc. A cv. with an *R*-gene or an *R*-gene combination remains uninfected as long as a compatible

Aardevo Exhibit 1013
Page 0083

Tab. 16: Gene-for-gene system with *Phytophthora infestans*. Dominant major genes, each conveying specific hypersensitive resistance of the host (*R*-genes), are matched by genes for specific pathogenicity of *P. i.*

Gen-für-Gen-System in P. i. Dominante Hauptgene, von denen jedes eine spezifische Überempfindlichkeitsresistenz des Wirtes überträgt (R-Gene), werden durch Gene für spezifische Pathogenität von P. i. überwunden (BLACK 1953)

pathotypes of *P. i.* genes for hypersensitivity	0	1	2	1,2 etc.
r	+	+	+	+
R_1	−	+	−	+
R_2	−	−	+	+
R_1R_2	−	−	−	+
etc.				

+ = susceptible – anfällig; − = resistant

pathotype does not show up. Elven *R*-genes are known so far. A range of test clones with different *R*-genes allows classification.

The *P. i.* population of a field starts with few spores surviving on the surface of stored tubers or groundkeepers and builds up a spectrum of pathotypes during the vegetation period. It is not sufficient to explain the diversity of this spectrum of pathogens by the usual mutations and re-combinations because there seems only one mating type to exist all over the world, with the exception of Mexico. Selection by potato genotypes certainly plays a role in manifestation of the pathotypes. However, pathotypes also arise in the absence of selecting host counterparts (MALCOLMSON & BLACK 1966, MALCOLMSON 1970).

The number of complex pathotypes encountered in isolates from field plants has increased continuously during recent decades (SCHÖBER 1983). The most frequent ones are complex pathotypes matching the host genes R_1, R_2, R_3 and R_4 in different combinations. The increase may be due to the rise in genetic variability among the newer cultivated genotypes. The lack of pathotype 0 is striking.

Genes for hypersensitivity are expressed in the sprout as well as in the tuber. But only in the tuber hypersensitive reactions are connected with the formation of phytoalexins. The reaction can be brought about by application of a spore suspension to the surface of tuber slices. The surface turns dark brown and necrotic in response to an incompatible pathotype. Necrotic reactions can also be followed with calli and protoplasts (DOKE & TOMIYAMA 1980 b). MÜLLER & BÖRGER (1940) detected phytoalexins as substances formed during hypersensitive reactions in the tuber which kill the parasite and the cells invaded by it. They are defined as low molecular weight antimicrobial compounds (OUCHI 1983). They accompany hypersensitive fungal and bacterial infections and mechanical injuries in tubers. They are to be met with in uninfected or intact tissue only as traces or not at all. The main phytoalexins of the potato are the sesquiterpenoids rishitin and phytuberin, while solavetivon and lubimin occur more rarely. They are formed as final products of the acetate-mevalonate pathway. Usually this pathway ends with steroid alkaloids such as α-solanin, α-chaconin etc.

Much work has been done to reveal the biochemical pathways in detail. For recent investigations and discussions see BAILEY & MANSFIELD (1982), KEEN (1982), OUCHI (1983), CLARKE (1983), KUC (1984), PANOPOULOS et al. (1984) and DARVILL & ALBERSHEIM (1984).

The following conception may arise. The synthesis of phytoalexins is mediated through elicitors. These are unsaturated fatty acids of the fungal cell wall. The elicitors react with potato lectin, i. e. hydroxyproline- rich glycoproteins, likewise fragments of the cell wall serving as receptors in the host cells. They induce the acetate-mevalonate pathway to produce phytoalexins. These accumulate in the cells which die off together with the fungus.

Aardevo Exhibit 1013
Page 0084

The result is incompatibility. The synthesis is ± inhibited when specific water soluble glucans (long glucose chains) of specific pathotypes block the receptor sites. Consequently, fewer toxic terpenoids are formed or even none at all (compatibility). The *R*-gene products of the host seem to control the receptor sites. Each pathotype thus possesses a pathogen-unspecific system eliciting the phytoalexin and on the other side, a specific one to block phytoalexin synthesis in case it meets with the specific receptors of the host.

It seems that a hypersensitive reaction needs not necessarily be connected with phytoalexin accumulation.

A complete understanding of the hypersensitivity reaction has not yet been reached. The sequence of different steps, timing of synthesis and detoxification of phytoalexins and perhaps other involved compounds may play a role (VANETTEN et al. 1982). SCHÖBER (1980) and others found no clear differences in rishitin accumulation when infecting tuber slices with compatible and incompatible pathotypes.

Breeding for hypersensitivity, as should be remembered, offers no solution of the late blight problem. Every *R*-gene or combination of *R*-genes introduced into cvs. stimulates the selection of an appropriate pathotype of the fungus. The insignificance of the *R*-genes becomes dramatically clear when the resistance levels of cvs. carrying *R*-genes are compared with those without *R*-genes. 64 % of the cvs. with *R*-genes fall into the group with a resistance score between 1 (highest resistance) and 5 (medium resistance). Nearly the same percentage (62 %) of cvs. without *R*-genes belong to the same group according to the variety list of STEGEMANN & SCHNICK (1985). As a consequence, parents for breeding are chosen in practice without regard for whether they carry *R*-genes or not. However, the possibility cannot be excluded, that *R*-genes may play a role when particular combinations with polygenes are given. E. g. the *S. demissum*-hybrid MPI 19268 carries the gene R 10 and at the same time possesses a very high field resistance (Anon. 1983 b).

The field resistance consists of several components (VAN DER ZAAG 1959, TOXOPEUS 1964 and earlier, UMAERUS 1970, HODGSON 1961, ULLRICH 1976, UMAERUS & LIHNELL 1976, NANDRIS et al. 1979, NILSSON 1981). Even before a parasitic contact is established, the host is active in influencing the mobility of the zoospores, the place of encystation and the ability to germinate. It follows the differences in the time lag up to the appearance of the first lesions (penetration), in the number of lesions, in the amount of lesion growth, in the production of conidia which can be late and few (sporulation index), and in the rapidity of spread from a central disease focus in the field. Resistant cvs. and wild species vary greatly in the expression of the different components.

Field resistance is controlled by many interacting genes (BLACK 1970, KILLICK & MALCOLMSON 1973, TAI & HODGSON 1975 and MALCOLMSON & KILLICK 1980). The mean resistance of a progeny was generally below the parent mean. However, in some progenies the growth of mycelium in the leaf was 5–50 % restricted compared with the mean of different parent combinations. Besides the general combining ability, specific combining ability was also found. Often tests of progenies of resistant parents showed a shift in the direction of resistance. Reciprocal differences turned up in *S. demissum* back-cross hybrids, according to GOREA et al. (1981). The resistance has a particular relation to maturity. The more advanced the life cycle, the more susceptible is the plant to an infection. Late maturing cvs., therefore, are more resistant.

Several methods have been developed for the assessment of field resistance of the leaves (NILSSON 1981). As a general pretest seedlings are infected in the field in July with a zoospore suspension mixed from different pathotypes, followed by sprinkler irrigation. The diseased leaf area is the measure of resistance. The standard test used for greenhouse screening was established by HODGSON (1961). He punched discs out of the leaves of field plants shortly before flowering. These were put into open boxes and sprayed with a suspension of a zoospore mixture, mostly of the pathotypes 1.2.3, 1.3.4, and 1.4.11. The correlation of these and of experimental greenhouse results with the field observations is not without problems partly because of the high interference of environmental factors (HODG-

Aardevo Exhibit 1013
Page 0085

SON 1962, LAPWOOD 1963, GUZMAN 1964, MAIN & GALLEGLY 1964, UMAERUS & LIHNELL 1976, PIETKIEWICZ 1976, GARCIA et al. 1977, STEWART et al. 1983). In an appropriate selection among glasshouse seedlings CALIGARI et al. (1984) obtained reliable results and could sort out susceptible seedlings as a pre-test (compare WASTIE et al. 1983). A relatively constant infection pressure by a broad spectrum of pathotypes necessary for field tests, prevailed in the Toluca valley near Mexico city. Field tests of prominent clones from international breeding stations were performed there over several decades (FRANDSEN 1958, NIEDERHAUSER 1972). Similar conditions are present now at the Experimental Station »La Selva« of the Instituto Colombiano Agropecuaria in Rio Negro near Medellin (ESTRADA-RAMOS et al. 1983 a).

Tuber resistance did not attract an equal interest, because it was believed to be present at a satisfactory level in most cvs., although severe damage can occur. As in the case of sprout resistance also breeding for tuber resistance is based today on field resistance, controled by minor genes. LAPWOOD (1965) developed a tuber test for field resistance which was used in modified form by SCHÖBER & HÖPPNER (1972). Tuber slices were infected with 50 zoospores 24 hours after cutting. Two days later, the development of the air-mycelium was determined. Because of the time lag between cutting and infection, the resistance factor of wound healing is included in the screening results. WALMSLEY-WOODWARD & LEWIS (1977) inoculated the eyes and lenticells. HOWARD et al. (1978) screened the tuber resistance by infection of microgroups of plants in the field and held them under constant sprinkling. Field resistance of leaves and tubers is related in the same genotypes only loosely (NILSSON 1981, SCHÖBER 1981, see also STEGEMANN & SCHNICK 1985).

Studies of the biochemical causal factors of the field resistance of tubers were made by DOKE & TOMIYAMA (1980). They observed that protoplasts or calli of cvs. died off after different time intervals when homogenate of mycelium of *P. i.* was added to the culture medium. The intervals reflected the gradation in field resistance of the cvs. A relation of the field resistance to rishitin content and its formation after infection could not be found (SCHÖBER 1980).

Another approach centers around the partly brown phenolic compounds such as lignin, suberin, callose a. o. found together with phytoalexins after wounding the surface layer of tuber slices or other tissue. They reduce the activity of several enzymes, hamper the penetration and later the growth of the fungus, can lead to death and are sometimes correlated with field resistance (SCHÖBER 1971, FRIEND 1973, CLARKE 1983, MCLAUGHLIN 1983, HOHL et al. 1984). HOHL et al. (1984) found the browning inversely correlated to cell-wall degradation (= protoplast yield) of cvs. and wild species. STOLLE & SCHÖBER (1984) isolated a toxin of 20.000 dalton from culture media of P.i. The toxin caused browning, dying off and phytoalexin accumulation when put onto the surface of tuber discs. This reaction, however, was neither related to the kind of R-genes nor to the degree of field resistance. The toxin diminishes also the growth rate of shoot tips and calli cultured in axenic media (WENZEL et al. 1984 a, WENZEL 1985).

Although the history of resistance breeding in the case of *P. i.* is fascinating, its results are disappointing. The resistance type of hypersensitivity had broken down after about 1932 when cvs. carrying *R*-genes became prevalent in the field. As an alternative, it was aimed to transmit the high graded field resistance likewise present in wild species such as *S. demissum, S. stoloniferum, S. vernei* and *S. verrucosum* to cvs. However, after 4–6 back crosses only a small part of the original resistance of the wild species remained. TAZELAAR (1981) has impressively shown the loss of resistance in *S. verrucosum* back-crosses. And, indeed, compared with pure ssp. *tuberosum* cvs. the many *S. demissum* back-cross cvs. hardly manifest any higher field resistance (see STEGEMANN & SCHNICK 1985). This may be due partly to the rare occurance of segregants combining the many genes necessary for quality and yield with those of *P. i.* resistance. But another reason of equal importance may be that the complex of field resistance components inherited by minor genes effects has been dispersed in the course of back-cross breeding (BLACK 1970).

Aardevo Exhibit 1013
Page 0086

A solution of the *P. i.*-problem can be found in planned reassembling of the components. In order to improve a »quantitative« trait, the practice is often followed of simple accumulation minor genes by intercrossing parents with high resistance. The fact is thereby neglected that groups of minor genes can initiate qualitatively different processes. The proposed reassembling means a planned combination of the single components of the field resistance. An understanding as to which component from the original source (mostly *S. demissum*) in the available resistant parent genotypes has been left over and is responsible for their resistance is taken for granted. In fact, investigations of this kind exist. PIETKIEWICZ (1976) studied the differences in the expression of the single components in Polish cvs. He found in some cvs. the resistance to infection to be predominant, in others, the resistance to spread and to sporulation. SCHÖBER (1981) observed in leaves of ssp. *tuberosum* and *S. gourlayi* high susceptibility and high sporulation index. In S. *fendleri* high susceptibility was combined with low sporulation index and in *S. bertaultii* both were low. A broadening of such studies could perhaps lead to the assumption that cvs. based on different wild species may differ in the predominance of certain components.

Cvs. having received their resistance from different sources can be grouped as follows:
1. pure ssp. *tuberosum* cvs. To this group with grading $\leqq 4$ (STEGEMANN & SCHNICK 1985) belong: Ackersegen (3), Carmen (4) and Verena (3) of the Federal Republic of Germany, Alpha (3), Bevelander (3), Furore (3), Gineke (3), Irene (3), Libertas (3), Pimpernel (2), Record (4), Urgenta (4), Woudster (4) of the Netherlands, Calrose, Saranac, Sebago etc. of the USA;
2. A second group comprises cvs. and breeding lines ex *S. demissum* or *S. demissum* plus ssp. *andigena*. The cvs. enumerated at the beginning of this Section belong here, as well as the majority of the newer *P. i.* resistant cvs;
3. A third, rather heterogenic group, consists of cvs. whose resistance originated from *S. demissum* and additionally from the resistant wild species *S. stoloniferum, S. vernei* and *S. verrucosum*. 24 out of 40 cvs. of this group in the Federal Republic of Germany are graded as 2–4 (see STEGEMANN & SCHNICK 1985).

Generally, cvs. of ssp. *andigena* are susceptible (VAN SOEST & SEIDEWITZ 1981), but exceptions were found. Among the wild species, however, a wealth of resistant forms exists (GRAHAM 1963, TOXOPEUS 1964, UMAERUS & STAHLHAMMER 1969, SCHÖBER 1981, TAZELAAR 1981, VAN SOEST 1983, VAN SOEST et al. 1983 a, b, HOHL et al. 1984): *S.* × *berthaultii, S. bulbocastanum, S. chacoense, S. chiquidenum, S. circaeifolium, S. fendleri, S. hjertingii, S. microdontum, S. multidissectum, S. papita, S. pinnatisectum, S. polyadenium, S. polytrichon, S. quimense, S. stoloniferum, S. tarijense, S. vernei* and *S. verrucosum*. Most of these species are split into resistant and susceptible provenience. Some of the species belong to Mexican Series and are difficult to cross with *S. tuberosum*. HERMSEN (1982) could combine several resistant wild species with ssp. *tuberosum* to form complex hybrids: *S. bulbocastanum – S. pinnatisectum – S. polytrichon – S. tuberosum* and *S. verrucosum – S. etuberosum – S. pinnatisectum – S. tuberosum* – as well as *S. acaule – S. bulbocastanum – S. phureja – S. tuberosum* (ABPT). The latter hybrid seems to be particularly outstanding in its resistance to *P. i.* (Anon. 1983 b). VAN SOEST & SCHÖBER (1983) succeeded in creating hybrids of the constitution cv. Olympia × *S. fendleri* × *S. hjertingii*. It must be expected that part of the resistance of these species will probably after some back-crosses, fade away in a similar manner to that experienced with *S. demissum, S. verrucosum* etc. There is nevertheless, as outlined above, the possibility of adopting the strategy of recombining the resistance by crossing those breeding hybrids and cvs. that offer complementary components. This could be achieved in the classical way by intercrossing differently based resistant back-cross hybrids or more methodically according to the analytic-synthetic breeding scheme (DE, MAINE 1982). In the latter case, dihaploids would have to be extracted out of differently based resistant back-cross hybrids and selected dihaploid genotypes than must be combined with resistant tetraploids. Selection of *P. i.*-resistant somaclones is described in Section 5.2.2.

Aardevo Exhibit 1013
Page 0087

7.5 Wart, Synchytrium endobioticum (Schilb.) Perc.

The fungus forms cauliflower-like tumours on the tubers and lower parts of the plants. It propagates in summer by zoospores from sporangiums of the sori and otherwise by resting sporangia. These can survive in the soil for more than 30 years.

The disease is spread above all in humid mountain elevations of maritime climates in Central and Northern Europe and similar parts of the world. It was a feared disease in the first decades of the century, occasionally destroying the total harvest of a field. Because genes for resistance had been introduced into the European cvs. very early (Ross 1958 a, b), a majority of the cvs. remained unattacked. In about 1941 an epidemic broke out and, moreover, pathotypes developed attacking the hitherto resistant cvs. Legislative measures were taken and the growing of susceptible cvs. forbidden. The disease then retreated more and more in the following years, the measures were suspended partly in 1966 and susceptible cvs. returned to the official lists. The differential scheme of the four pathotypes most important in Europe, is gtiven in *Table 17.* The following pathotypes are met within the Federal Republic of Germany: P-1 in ca. 1 % of the diseased fields, P-2 in ca. 32 %, P-6 in ca. 65 % and P-8 in ca. 2 %. The remaining 13 pathotypes have been found only very sporadically (LANGERFELD 1984 e).

Two methods are available for testing the resistance (LANGERFELD 1984 a, b) which both are applied in the official tests. KOTTHOFF and SPIECKERMANN inoculated tuber pieces with rotten old tumour tissue containing the diploid permanent sporangia. In this way a type of resistance is tested that may be similar to the type of field or infection resistance met with other pathogens too.

The method of GLYNNE and LEMMERZAHL, with a more widespread application, measures the necrotic reaction (hypersensitivity). Tuber eyes are covered with haploid spores from summer sori of fresh wart tissue. The inspection three weeks later allows a gradation into six groups with decreasing necrotic response between rapid dying off of the primarily infected cells and almost undisturbed growth of the sori. Genotypes reacting with types 1, 2 and the rarely occuring 4 are categorized as resistant I, those with types 3 as resistant II and those with types 5 and 6 as susceptible.

STACHEWICZ (1983) used microtubers from in vitro plantlets for screening. First results showed a reliability for this method which would save on field experiments and could possibly be performed in most winter months.

FREY (1980) developed a seedling test. Seedlings in Jiffy pots are inoculated with tumour tissue. Cycocel is sprayed over the seedlings in order to induce tuber formation. New tumours are formed on tubers and stolons of the susceptible genotypes after 4–9 weeks.

The genetics of the resistance are favourable for the breeder, but the interpretation of the segregation patterns is difficult. Crossing of susceptible parents with those resistant to pathotype 1 results in a 10–80 % resistant progeny, whereby the higher percentages prevail. Even when susceptible parents are crossed, resistant seedlings can result.

Tab. 17: Differentiation of the four most important pathotypes of wart
Differenzierung der wichtigsten Krebspathotypen (LANGERFELD 1981)

differential cvs. *Differentialsorten*	pathotypes – *Pathotypen* 1	2	6	8
Irmgard	–	+	+	+
Saphir	–	+	–	–
Ultimus	–	–	–	–

1 = common pathotype – *allgemeiner Pathotyp* 2 = pathotype »Haas« (Bayern) 6 = pathotype »Olpe« (Westfalen) 8 = pathotype »Bronnzell« (Hessen). – = resistant, + = susceptible – *anfällig*

Aardevo Exhibit 1013
Page 0088

FRANDSEN (1958) explains the situation with the involvement of two resistance types with possibly different inheritance and with arbitrarily fixed limits between resistant and suscpetible progeny.

MARIS (1973) considers one dominant gene as responsible for the resistance, whilst three other complementary genes suppress the effect of the first one. This concept could explain the occurrence of resistant segregants in progenies of parents both of which are susceptible.

Also SCHEIDT & HUNNIUS (1981) like ROTHACKER et al. (1974) see the basis of the inheritance in one dominant gene that must be present for any necrogenic resistance. They studied the genetics of the resistance to the pathotypes 1,2 and 6 in progenies of the clone MPI 50.247/2 as the resistant parent. Screening was performed with the two described laboratory methods as well as with field trials. The progeny was divided into nine rating groups. A 1 : 1-segregation could be established when the groups 1 plus 2 were plotted against 3–9. The progenies were preselected for yield and quality. The segregation figures vary in different years by reason of edaphic and climatic differences. They vary also by the used susceptible and resistant parent and can be accounted for by the additional effect of minor genes. Minor genes seem to be responsible when for example 34 % of the progeny was resistant to both pathotypes 2 and 6, and 17 % only to one of them. All genotypes with resistance to P-2 and P-6 are also resistant to P-1 but not vice versa.

One of the sources of wart resistance is the old cv. Flourball (Ross 1958 a). Resistance to P-1 and other pathotypes is here often correlated with susceptibility to P-8 and red colour of the tuber skin. This correlation is transmitted to its progeny cvs. Ultimus, Urgenta, Désirée and Pink Perl. Another source of resistance to different pathotypes is the clone BRA 9089 originated from crosses which combine a Chilean cv. of ssp. *tuberosum,* the Polish cv. Switez and a cv. from Frankonia. Different spectra of resistance to pathotypes are conferred on cvs. Galina, Judika, Oda, Ora, Tondra and Xenia. A further source of resistance is the wild species *S. acaule.* It conferred resistance to cv. Saphir (all pathotypes except P-2) via the back-cross hybrid MPI 44.1016/24. The origin of cv. Barbara (P-1, 2, 6, 8) cannot be traced back with certainty. A certain level of resistance to different pathotypes is also found in the nematode resistant cv. CPC 1673 and another Bolivian cv. of the ssp. *andigena.* The resistance in the latter case is of the type of field resistance. It was introduced into Canadian cvs. as e. g. Brigus (PROUDFOOT, pers. comm.). LANGERFELD observed a certain degree of resistance to the pathotypes 2,6, and 8 originating from CPC 1673 in the German cvs. Amalia, Gelda, Maja and Titana. For the pattern of resistance of other cvs. see LANGERFELD (1984 a).

Resistance to wart is also found in other wild species (VAN SOEST & SEIDEWITZ 1981). However, because resistance is present already in so many cvs. and breeding lines, a new introduction of wild species for this purpose seems unnecessary.

Most of the contaminated places are gardens and other areas with less regular crop rotation. It is, therefore, recommended to combine resistance to wart with resistance to nematodes which is a disease of equal importance for a potato crop grown in gardens.

7.6 Scab, *Streptomyces scabies* (Thaxt.) Waksman et Henrici

Scab prefers sandy soil. It is transmitted through the soil and hardly ever through the tuber. Scab reduces the quality of the tubers and thus their commercial value. The demand for good appearance of the tubers is higher today because more potatoes come to the marked, washed and packed in transparent foil.

The ubiquitous parasite infects the thickening ends of the stolons. The infection is favoured by a higher pH value and dryness of the soil. The critical period for the infection lasts 3–4 weeks after the beginning of the growth of the tubers (LAPWOOD & HERING 1970, WIERSEMA 1974). Three different symptoms are distingusihed: shallow (plain), buckel and deep scab. JELLIS (1977) stated that these symptoms are not due to genetically different infects but express the severity of the disease and vary according to environmental factors.

Aardevo Exhibit 1013
Page 0089

Pathotypes with different varietal specifity have not been observed so far. However, single isolates differ in aggressivity (BJØR & ROER 1980).

Tests for resistance in the field have to take into account differences of soil alkalinity and of rainfall during May–June (LAPWOOD 1972). Usually the ditch method of NOLL (1968) is applied. Ditches are filled with scab soil, i. e. soil in which scabby tubers have been grown, or, the soil or sand is mixed with aritificial scab cultures. Procedures for screening in pots have been developed by BJØR & ROER (1980). JELLIS (1975) performs the field tests in a polythene tunnel. GUNN et al. (1983) prefer the glasshouse pot inoculation to the field methods. Seedlings can be screened in boxes filled with sand or vermiculite to which nutrient solution of pH 7 and a spore suspension is added.

The gradation of resistance in field trials is performed by counting the number of attacked tubers and the extent of the diseased area. Exact measuring is not superior to a general visual judgement (DOWLEY 1972). A division into 10 ratings would be possible.

KRANTZ & EIDE (1948) concluded on one single dominant major gene. The degree of resistance should increase from simplex up to quadruplex condition. Other variations in the segregation figures are attributed to minor gene effects. CIPAR & LAWRENCE (1972) extracted dihaploids from the resistant cv. Hindenburg and the medium resistant cv. Avon. 74.1 % of the Hindenburg- and 37.2 % of the Avon-dihaploids fall into the classes one and two (of five). HOWARD (1978) concludes that more than one gene pair controls the resistance.

Well known as producing a scab resistant progeny are many older cvs. such as Ackersegen, Carmen, Hindenburg and Jubel as well as Cayuga, King Edward, Ontario and Pentland Crown and several new ones (see STEGEMANN & SCHNICK 1985), e. g. Jessica, Roxy and Tempora from the Federal Republic of Germany with broader distribution.

7.7 Black scurf, *Rhizoctonia solani* Kühn

The fungus is a heterokaryont. The natural populations are composed of different genotypes. *R. s.* lives as a saprophyte in the soil and as a parasite on the surface of tubers or on the lower parts of the stalks. The parasitic phase is favoured by cold and humidity. The fungus attacks roots, stolons and young sprouts. The decay spreads and the tubers remain small and become more numerous. At the same time the characteristic rolling of the younger leaves develops. The mycelium of the tuber surface at the end of the growing season forms sclerotia (pox). They can also develop during storage. New inoculations mostly start from the sclerotia but also from the soil when emergence is retarded. A small (in certain trials up to 15 % of the tuber surface) infection with pox need not always lead to an inoculation, especially when the emergence is rapid. The germs become resistant as soon as they come to daylight. The final attack is determined very distinctly by environmental conditions (JAMES & MCKENZIE 1972, FRANK & LEACH 1980). PLAMĂDEALĂ (1978) investigated the yield depression of 16 cvs. after having added mycelium to the tubers at the moment of planting. The less susceptible cvs. were Elba, Magura, Merkur, Procura, Spartaan and Ulster Chieftain.

Breeding for resistance is still in its infancy because the etiology and performance of the disease was for a long time insufficiently known (ZACHMANN 1972).

A standard inoculation technique was developed by CHAND & LOGAN (1981). They covered tuber pieces carrying 2–3 cm long germs with agar slices from mycelium cultures and planted them in plastic pots.

SPENCER & FOX (1978) tested the pathogenicity of the mycelium from 89 isolates of slcerotia on leaves of several cvs. They found not only differences in the frequency of the leaf infections but also in the resistance of the cvs. 100 % of the leaves of the cv. Record, but only 45 % of cv. Golden Wonder, became infected by a mixture of three isolates.

It is assumed that the actual resistance is a combination of different components. HOFFERBERT et al. (1953) pointed to the differences in the ability of the cvs. to regenerate roots and stolons. Another component may be the rapid development in the first growth

Aardevo Exhibit 1013
Page 0090

phase. The different components and their genetics will presumably have to be investigated first before a planned breeding for resistance can begin. For selection among somaclones see Section 5.2.2.2.

7.8 Resistance to tuber damage and to tuber storage diseases

Previously neglected tuber impairments are of increasing interest today. Between their formation in the soil and their utilization by man the tubers can suffer from several kinds of serious impairments and injuries. These are apt to discredit the potato as a food intended for the table.

Endeavours to control the damage include improvements in the mechanical operations of the harvest, handling in store and during transport on the one hand and by breeding on the other are continuously intensified (STRICKER 1984).

It is to distinguish between injuries caused mechanically and those caused by parasites, in particular, by species of *Fusarium, Phoma* and *Erwinia.* Both groups of injuries are responsible for weight and other losses during storage, in the course of industrial processing, by utilization in the kitchen, or as seed potato. The extent of external and internal tuber damage is related to the genotype (HUNNIUS & SPECHT 1971, MUNZERT & SCHEIDT 1978) as well as to environmental factors (SPECHT 1968, PÄTZOLD & DAMBROTH 1970, HUNNIUS 1971, HUNNIUS et al. 1969, 1972. HUNNIUS & MUNZERT (1976) have shown that the component of variance due to variety is between 52 and 56 % and due to environmental factors between 20–22 %. Thus, the composition of the genotype is more decisive for the resistance to damage than the environment.

7.8.1 External tuber damage

LEPPACK (1984) divides mechanical tuber damage into three groups 1. damage inflicted by blow or pressure during harvest and transport. Within 24 hours tissue 2 mm under the skin turns from red over blue to black. After some weeks a grayish mass of dead tissue is formed. This effect is favoured by temperatures below 8–10 °C during harvest. 2. black spots, occurring deeper in the tissue, are the consequence of ageing and drying, promoted by a storage temperature being too high and the air in the boxes too dry. The tuber tissue is not destroyed. 3. depressions of the tubers in the store which are the result of pressure from tubers laying over them.

Resistance to external tuber damage is greatly influenced by ontogenetic and environmental factors. Firstly, there is a relationship to maturity class (SPECHT 1968, GALL et al. 1967, HUNNIUS & FUCHS 1970, HUNNIUS & SPECHT 1971). MUNZERT & HUNNIUS (1978) tested 133 cvs. during the period 1965–1977 and found that those in the mid-late maturity group were especially damage prone. Varietal characteristics of the haulm and tuber are also important (SPECHT 1968, HUNNIUS 1971). Favorable for damage free harvest is rapid early growth and rapid and uniform senescence of the standing haulm. The tubers should be closely crowded at the foot of the plant and easily loosened from the stolons; if their position is too high they will grow out from the ridges and be more prone to damage. If possible, they should be round-oval in shape; a round tuber moves more easily over the elevator, whereas a long-oval shape is open to greater damage from rolling as the crop moves along the web. In a given variety, large tubers are always more severely damaged than small ones. Well known is the disastrous influence of lower temperatures during harvest (HUNNIUS & MUNZERT 1976, GRAY & HUGHES 1978). COLE (1980) recommends the breeding of cvs. which can be harvested before the temperatures falls below 8 °C.

In order to assess true resistance an ordinary harvest with a commonly used harvester and handling operations must be carried out with large amounts of tubers. The crop must be grown on different soils, and the trials extended over several years (HUNNIUS & SPECHT 1971, HOLDEN 1981). After harvesting, the tubers should be stored for at least 6 weeks under uniform conditions before assessments of damage are made. The number and weight of the

Aardevo Exhibit 1013
Page 0091

damaged tubers is stated. The mean value of different cvs. or years or treatments included in a trial is set = 100. The deviation of the single cv. or treatment from the mean value denominates the degree of resistance. Grade 1 = 30 % of the mean is considered as very slight damage or high resistance, grade 5 = 90–110 % is characteristic for medium resistance and grade 9 with values > 170 % means very high damage and susceptibility (HUNNIUS & FUCHS 1970, WININGER & LUDWIG 1974). A peeling test evaluates the degree of external injuries (SPECHT 1968): injuries of < 1.7 mm depth are recorded as no damage, between 1.7 and 5.1 mm as slight damage and > 5.1 mm as severe damage.

Such harvester and storage trials cannot be made with younger breeding lines where only a limited amount of tubers is available. Methods applicable to smaller tuber lots were therefore developed to screen for distinct components of the resistance.

Many tests are in use in order to assess tuber traits responsible for resistance/susceptibility. No satisfactory results about resistance could be gained by FUCHS (1971) with the damage drum and by measuring the shear strength with special equipment. WEBER et al. (1981), however, find the damage drum test a very useful method, even to distinguishing between genotypes with stable and unstable reactions to environmental changes. The authors measured the degree of damage by estimating the amount of starch that can be washed out from the injured tubers. HUNNIUS & MUNZERT (1972) and MUNZERT & HUNNIUS (1974) applied a texture tester to test the firmness of the flesh and obtained quite good relationships between experimental and field results using multiple regression analysis.

In other experiments, steel cylinders were dropped from a fixed height. This method delivered satisfactory results in trials by UMAERUS & UMAERUS (1976), BAILEY (1980) and JÖNSSON & FRIDELL (1981). Resistance to tuber impact measured with the ball-drop test is inherited by minor genes, as can be concluded from experiments by JASTRZEBSKI (1983). Seedlings superior to the best parent were found in each combination. However, a susceptible parent reduces the resistance of a progeny severely.

Penetrometer measurements have been made by MEINL & EFFMERT (1966), KILLICK (1972) and BLIGHT & HAMILTON (1974). These authors were nearly unanimous in concluding that penetrometer data cannot be used alone to predict susceptibility to injury.

GALL et al. (1967) developed a rebound pendulum for testing damage susceptibility early in the breeding selection procedure. FUCHS (1971) does not consider that the pendulum alone gives valid results, but WEBER et al. (1981) concluded that the rebound pendulum is, indeed, quite useful for early selection. GRANT & HUGHES (1985) developed pendulum equipment that allowed them to measure the absorbed energy and to predict the resistance to damage. The method is based on the dynamic tissue strength, i. e. the resistance to cell wall fracture. The authors connected the equipment to a microcomputer. – Measurement of energy is also the purpose of an apparatus where potato cores are extruded by a hydraulic ram through a multihole plate (MCRAE et al. 1984).

MEINL (1972) used two devices, one to measure radial compressibility and the other to measure the rebound rotational property as parameters for assessing the interactions of elasticity and mass. Finally PORTEOUS & MUIR (1981) describe an instrument which by measuring the spectral reflectance of tubers allowed them to differentiate between 11 types of damage, including those caused by parasites.

7.8.2 Blue spot (bruising)

The coloration is produced by enzymatic hydrolysation and oxidation of the amino-acid tyrosine and other phenolic substances (MÜLLER 1979). Resistance to blue spot differs greatly between the cvs. (GRASSERT & PAPENHAGEN 1979). About 40 % of the difference is genetically determined (AEPPLI et al. 1979). Late maturing cvs. and those with larger tubers and a high dry matter content are most sensitive but there are exceptions (COLE 1980, BAUMGARTNER & KELLER 1983). Blue spot is also influenced by the physical constitution and the chemical composition of the tuber and largely by environmental factors (HUGHES 1974, HUNNIUS & MUNZERT 1976, EFFMERT & SCHÜLER 1978, AEPPLI et al. 1979, KILLICK &

Aardevo Exhibit 1013
Page 0092

MacArthur 1980). Baumgartner et al. (1983) studied the resistance to blue spot and the stability of this trait over several years and sites by shaking hand dug tubers in wooden boxes and by using the drop test. They applied this method to 19 cvs. from the Swiss list of cvs. and found a good differentiation among them. The most resistant ones turned out to be at the same time the most stable.

There are several physical and chemical factors controlling the resistance to blue spot. The influence of each of them on resistance varies among the cvs. (Gray & Hughes 1978). Baumgartner et al. (1983) find on average the following correlation coefficients measured with freeze dried substance: dry matter (underwater weighing) % r = 0.47, dry matter % r = 0.55, starch % r = 0.44, cell size r = − 0.29, chlorogenic acid mg/100 g r = 0.37 (related to fresh substance r = 0.43), citric acid % r = − 0.23, K_2O % r = − 0.33 and tyrosin mg/100 g r = 0.55.

Baumgartner et al. (1983) recommend the selection of genotypes with low content of chlorogenic acid combined with a low tendency to discolouration of the raw pulp.

Umaerus & Umaerus (1976) and Cole (1980) point to the fact that cvs. react differently when several methods are used to test their resistance. This means that the composition of the complex responsible for the final overall resistance differs among the cvs. Because the decisive component for the resistance of a distinct breeding parent is usually not sufficiantly understood, a planned breeding is very difficult. Thus, as in similar cases of traits controlled by minor gene effects, it is recommended that the best genotype be used as at least one of the parents and that the use of a genotype with above average susceptibility as the second be avoided.

7.8.3 Dry rot, *Fusarium solani* var. *coeruleum* (Sacc.) Booth and gangrene, *Phoma exigua* Desm. var. *foveata* (Foister) Boerema

The fungi of the genera *Fusarium* and *Phoma* are mainly wound parasites and develop during storage. Their discrimination is sometimes difficult. Often an association with *Erwinia* is observed (Langerfeld 1978, 1983). Sources of infection are nearly ubiquitous, e. g. damaged and undamaged seed tubers, rain, aerosoles, etc. The relative importance of the different fungi varies from one region to another. *Phoma exigua* var. *foveata* is the principal cause of tuber rots in Great Britain and Ireland (Boyd 1972). *Fusarium coeruleum* is the dominant pathogen in the Federal Republic of Germany and the USSR, whereas *Fusarium sulphureum* is most important in the German Democratic Republic (Pett et al. 1977) and in Poland.

Because the pre-existance of wounds is important for the infection, resistance of the tuber to damage gives a high protection (Ulrich & Möller 1977). Langerfeld (1978) attributes to this factor as a breeding aim a higher priority than to tuber pathogen resistance.

Different methods have been developed to test for resistance to *F. coeruleum*. Leppack (1981) developed a method for storage susceptibility close to practical conditions. Tubers are agitated for 1 min on a grading machine and at the same time inoculated by spraying with a *Fusarium* suspension. Wiersema (1977) worked with halved tubers whose cut surfaces were simply painted with inoculum. Horackova (1977) injured the rose ends of the tubers and then inoculated them with a specially constructed metal device. Langerfeld (1979) applied two methods. With the one method spores were applied to injuries made by a Philips' screw driver equally on each tuber of the different cvs. With the other method injuries were inflicted by a rebound pendulum. The amount of damage is related to the mechanical resistance typical for the cv. Inoculation is performed afterwards. The yearly deviations from the mean values are great. The correlation coefficient of the amount of decay by infection with both methods were 0.71 in 1976 and 0.48 in 1977. The correlation coefficients of the infection effect between the screwdriver methods and the frequency of rotted tubers (i. e. limited spread or localisation of the infection) was between 0.81 and 0.92 in different years. Some cvs. showed higher resistance with the pendulum method than could be expected from the results with the screwdriver method. Munzert & Hunnius (1980) like

Aardevo Exhibit 1013
Page 0093

LANGERFELD injured tubers with the screwdriver halfways between their ends to a depth and width of 7 mm.

The incidence of infections with Phoma exigua var. foveata in different cvs. and their relation to seed tuber, soil, climate, temperature before and after the infection were studied by LANGTON (1971), ROGERS & KILLICK (1975) and UMAERUS & UMAERUS (1976). The amount, type and severity of the wounds as entry points for the fungus determine the disease incidence strongly (ADAMS 1980). JELLIS (1982) in trials for resistance dipped washed tubers momentarily into the inoculum. After storing them in polythene bags at 10 °C for a week, he wounded the tubers on a reciprocating table covered with river gravel. The table was moved for 0, 30, 60 and 90 sec to produce different amounts of small crush wounds. The tubers were stored afterwards at 5 °C.

There was a significant positive correlation of the diseased area between damaged and undamaged tubers, stated after 40, 60 and 90 days. But the discrimination of the genotypes was not possible by assessing the proportion of diseased tubers (see also JÖNSSON & FRIDELL 1981). LANGTON (1971) infected tubers by inserting cores of mycelium from Petri dish cultures into wounds made by a cork-borer or twist drill. The radius, depth and score of the lesions were measured and a good correlation with commercial results was obtained when the experiments were performed at 10 °C. SCHEITZA (1983), in similar trials, assessed the resistance by weighing the excised lesions. The author observed differences in the pathogenicity of isolated lines of *P. e.* and a shift of the optimal temperature for growth during storage months from 4 °C to 20 °C.

7.8.4 Soft rot and black leg, *Erwinia carotovora* (van Hall) Dye

Erwinia carotovora comprises the ssp. *carotovora* and *atroseptica*. Both ssp. cause soft rot of the tubers, i. e. they turn the tubers wholly or partly to a slimy squash and cause the stalks to wilt. Both also cause black leg, but in moderate climates this disease is more often due to ssp. *atroseptica* (LAPWOOD & HARRIS 1982, LANGERFELD 1984 c, d, RADTKE 1983). Black leg means that the stems turn black and can be drawn out of the soil without difficulty. The stems are often slimy and rotten at heir base and in humid environments in upper parts of the stems as well. Often no tubers are formed. Very important is the occurrence of latent contamination, as often happens with daughter tubers of infected mother tubers.

The bacteria are spread to the tuber surface by water in the soil, by rain and dipterous insects (LAPWOOD & HARRIS 1982). The rotted mother tuber is assumed to be the main source of contamination. The bacteria are present but mostly inactive (latent) on the tuber surface, in the lenticells and in the vascular bundles of the tuber. They become virulent or are favoured in development through wounding, high water potential, high CO_2- and low O_2-content and higher temperatures (NAUMANN et al. 1976, PÉROMBELON & KELMAN 1980, PÉROMBELON et al. 1980, FOX 1981, MAHER & KELMAN 1983, JÄGGI 1984). Pectolytic enzymes macerate the cell walls. Low oxygen content inactivates pectolytic enzymes or pectic substrates which stand the enzymatic disintegration. This leads to inhibition of wound healing and defence reactions. Also increased membrane permeability enhances bacterial growth due to leakage of nutrients (MAHER & KELMAN 1983). Cell wall degradation occurs in advance of the formation of phytoalexins and other metabolites which are believed by other authors to be responsible for resistance (compare GHANEKAR et al. 1984).

A simple method for detecting the bacteria on or in the tubers is putting single tubers in a plastic bag with water at 20–22 °C for 5–10 days. When soft rot lesions appear the tubers will be put on dry whilst rotting continued anaerobically (PÉROMBELON et al. 1980). An ELISA-method has also been developed (SUTULA et al. 1982).

Breeding for resistance to ssp. *atroseptica* has priority because it induces soft rot as well as black leg. Resistance of cvs. to soft rot caused by ssp. *atroseptica* was investigated by HAHN & SCHÜLER (1974) and HAHN (1974) and LELLBACH (1976). ZADINA & DOBIAS (1976) found a positive correlation ($r = 0.647$) between tuber soft rot and stem black leg (see LANGERFELD 1984 d). The cvs. Saphir and Sickingen were the most resistant among 100 cvs. HAHN (1974)

Aardevo Exhibit 1013
Page 0094

considers the testing of tuber for soft rot alone to be sufficient because black leg follows a tuber infection.

LELLBACH (1978) found resistance to soft rot to be controlled by minor gene effects, but the influence of environment was very high, making him sceptical of the success of breeding for resistance to soft rot. PFEFFER et al. (1974) did not share his scepticism. MUNZERT & HUNNIUS (1980) see a necessity to improve the resistance to soft rot and black leg by breeding and give black leg and *Fusarium* diseases a higher priority than soft rot.

Several screening methods to differentiate resistance have been developed, such as inoculation of entire tubers or of tissue cylinders with bacterial suspensions etc. HENNINGER (1965), HAHN (1974) and HAHN & SCHÜLER (1974) used the pinprick inoculation technique successfully. WASTIE (1983) used a medical »jet injector« to force a suspension into the tuber and obtained a better differentiation in the resistance of the genotypes than by inoculating tuber slices or putting the suspension into a drilled tuber hole. NAUMANN et al. (1976) and SIMON et al. (1984) infiltrated the bacterias into the lenticells under vacuum pressure.

As mentioned, it is necessary to breed separately for tuber soft rot and stem black leg. For studying resistance to black leg, infections are made in various ways: pinprick infections of young seedlings (DOBIAS 1976), infections of stem sections in test tubes and infections of stem bases with a jet injector (WASTIE 1983). LAPWOOD & GANS (1984), in field experiments, stab-inoculated seed tubers near the attachment of the stolons before planting. MUNZERT (1975) infected conical tuber pieces cut out of the tubers' rose-end. Inoculation was performed at the tip end of the tuber piece by means of a drawing-pin and filter paper soaked with a bacterial suspension. MUNZERT & HUNNIUS (1980) and MUNZERT (1984) inoculated tuber pieces of three week old eye plugs by putting bacterial suspension in a tuber hole drilled by a PHILIPS scewdriver. They obtained a relatively high correlation between the decyaed tuber piece and the development of black leg. Comparing their results for rotting after inoculation of the whole tuber with black leg incidence after inoculation of tuber pieces, they assume a resistance barrier when the disease passes over the transition zone from tuber to stem.

HOSSEIN & LOGAN (1984) inoculated tubers by inserting a wooden toothpick charged with bacteria into the rose end. Black leg incidence, growth and yield were observed in several cvs. over two years. Differences in tolerance were found. It should be mentioned that inoculation of sterile callus-born plantlets or tubers would prevent interference of latent germs. A progressive method perhaps is the inoculation of tuber slices through wounds. The cvs. Cara, Desirée, Pentland, Dell, Pentland Hawk and Pentland Squize (LAPWOOD & READ 1985) turned out to be the most resistant ones.

The rate of woundhealing seems to be an important resistance factor. It can be estimated by measuring the efflux of electrolytes from tissue in time intervals after damage (LOJKOWSKA & LEWOSZ 1984).

Even if some of the described labor methods allow a good differentiation among the genotypes they have to be compared with the results of practical handling when the respective genotypes have undergone the usual processes of growing, maturing, harvesting, transport and storage.

Although there is a strong need for resistant cvs., breeding at present is restricted to negative selection, i. e. highly susceptible seedlings are discarded and susceptible parents excluded. An alternative search for parents with specific combining ability would be useful.

Resistance to soft rot is not uncommon among the gene resource (PFEFFER et al. 1974, VAN SOEST 1983, CIAMPI & ANDRADE-SOTO 1984).

Aardevo Exhibit 1013
Page 0095

8 Breeding for yield and maturity type

Tuber number and tuber weight are the components of the single plant yield, whilst the yield of the crop is determined by additional factors.

Tuber number is genetically determined by the number of stems per plant and averages from 3 to 10. Each stem carries between 2.5 and 4.5 tubers with an overall mean of c. 3. Tuber size also is controlled by minor gene interaction (RUDORF & BAERECKE 1958, HOWARD 1970, 1978). There is a negative correlation between the number of stems per plant and the number of tubers per stem. In contrast, the number of stems and of tubers per plant are positively correlated. The size of the parent tuber as well as its pretreatment (the release of apical dominance) has an influence on the tuber number (HUNNIUS 1977 c).

Tuber initiation and growth is a complicated process controlled on the biochemical side by gibberellin (HAMMES & NEIL 1975). Short days accelerate tuber formation, whereas long days inhibit it. Short day sensitivity is dominant to day neutrality (MENDOZA & HAYNES 1977). The physiological condition of the seed-tuber (its physiological age) also markedly influences plant growth, stem and tuber formation, and maturation (MADEC & PERENNEC 1962). After the harvest, there is an inherent period of absolute rest varying from 3 to 15 weeks, depending on the genotype (MILTHORPE & MOORBY 1966, MÜNSTER 1975). The resting phase is followed by a latent germination (dormant phase; MÜNSTER 1975) where germination is inhibited by low temperature alone, and this phase marks the onset of physiological senescence. Tuber initiation begins about 15 and 25 days after emergence and genotypes may vary greatly in the time taken for the onset and subsequent duration of tuber formation. Adequate functional foliage is necessary for tuber development; there is a direct correlation between leaf-area and tuber yield up to a leaf area index (LAI) of 3 beyond which additional leaf area does not proportionately affect tuber formation (MILTHORPE & MOORBY 1966).

ENGEL (1964) considers that there are five key factors influencing the optimization of yield: 1. the rate of development of leaf tissue (the juvenile phase); 2. the quantity of fully functional leaf tissue; 3. its duration; 4. its productivity and 5. the rate of tuber development.

In the past most breeding efforts were directed towards the creation of cvs. adapted to temperate climates. As a result the yield level of cvs. grown in warmer climates is generally low. Although the yield can be raised by agrotechnical improvements and breeding it is doubtful whether the genetic potential of the potato would be sufficient to reach yields comparable to those of temperate climates (VAN DER ZAAG 1984).

A knowledge of the principles of crop formation, crop structure and crop physiology is a prerequisite for formulating breeding targets and determining selection criteria. Commonly, breeders aim to produce medium-sized tubers of a regular shape (to minimize waste); however, larger tubers are needed for »pommes frites« and small ones for the canning trade.

Early selection for yield among first year seedlings is risky because the decisive number of stems develop after some vegetative generations. Moreover, it is necessary to grow plants at an appropriate spacing to obtain a balanced selection for both tuber size and tuber number. There is a positive correlation between tuber number and yield on the average (KRUG et al.

1974 a). To minimize size variation, the aim should be to select plants with a short phase of tuber initiation followed by an even rate of tuber development (DAMBROTH 1975). VAN DER WAAL et al. (1978) and VAN DER ZAAG & BURTON (1978) suggested that yield could be increased by prolonging the duration of tuber growth and that this could be accomplished by a tolerance to low temperature that would allow earlier emergence and tuber initiation. MOLL & HEERKLOSS (1978) consider that selection for increased photosynthetic efficiency is a breeding resource that might be used to enhance yield.

There are differences of opinion about the optimal plant growth habit for improved interception of light energy that might contribute to an increased yield. Physiological considerations suggest that the growth habit should be upright, the stems rigid with only a few branches and the leaves erect (DAMBROTH 1975). ENGEL (1965) claims that plant habit can be predicted by a sprout test. SWIEŻYŃSKI et al. (1978) found that a high stem: leaf weight ratio may indicates a rapid phase of juvenile growth. Although some characteristics can thus be examined at an early stage, there is as yet no method of predicting the duration and functional ability of leaves.

There is a positive correlation between earliness and stolon length in seedlings (ENGEL & MÖLLER 1959). KRUG et al. (1974 a, b) considered that plant height had a predictive value and that tall seedlings were mainly late maturing. The time of maturity is polygenically determined (RUDORF & BAERECKE 1958, HOWARD 1970) and earliness tends to be dominant to late maturity (MÖLLER 1965, MARIS 1969).

Aardevo Exhibit 1013
Page 0097

9 Breeding for quality

Potatoes are used in many different ways. 51.7 % of the world potato harvest in 1975 was used for human consumption, 34.5 % for animal feeding, 3.5 % for starch and alcohol production, and 10.3 % was preserved for seed (VAN DER ZAAG 1976). Potatoes intended for consumption can be divided into those to be used directly and those to be processed. The processed part of the harvest is tending to increase, and the number of products is rising as well (HUNNIUS 1981, PUTZ et al. 1982, KEMPF et al. 1982). In 1982/83 the percentage of processed potatoes of those intended for human consumption in the Federal Republic of Germany was 27.1 % (PUTZ, pers. comm.).

Potatoes of top quality (WINIGER & LUDWIG 1974, HOWARD 1974, GRAY & HUGHES 1978, HOLDEN 1981) must possess the following distinct external tuber traits: medium size, good grading, good shape, flatness of the eyes, the right colour of skin and flesh, freedom from mechanically caused blue spots and damage, from growth cracks, greening, hollow heart, and scab, and resistance to washing. Internal quality comprises consistency, texture, mealiness, no darkening in the raw and cooked stage and good flavour. The protein content is low (and needs to be increased). However, the potato produces per ha more protein than other comparable crop plants *(Tab. 1)* and its biological value also ranks among the highest *(Tab. 2)*. Its index of essential amino acids (EAA) is 76–79. The content of vitamins and of minerals particularly K and Mg, is high.

The requirements for the properties of varieties to be processed vary according to the product aimed at *(Tab. 18)*. Besides tuber shape and size, the content of dry matter, starch and reducing sugars is important. High levels of reducing sugars lead to discoloration of crisps (chips) and french fries. Moreover, neither raw nor cooked potatoes should undergo rapid darkening. Potatoes to be used for the production of starch, alcohol and animal feeding must be high in starch content. Also of importance for this utilization are the viscosity, the amylase content and the size of the starch grain. Protein, resulting from starch manufacture can be recovered and used for feeding.

For any utilization, the tubers must not be too large. BURTON (1974) considers a weight between 150 and 200 g to be optimal. This should be connected with a good grading. A round-oval tuber fits most requirements, but for french fries and salads long-oval ones are preferred. A round-oval tuber is less susceptible to mechanical damage. The tuber shape is stated by measuring the index of length to breadth with a model, or visually with specimens (WINIGER & LUDWIG 1974). Inheritance studies showed that in some combinations, round is dominant over long (RUDORF & BAERECKE 1958) and in others, vice versa (HOWARD 1970). HOWARD (1970) found in some combinations a correlation between red skin and round shape. Flat eyes, of course, are desirable for all purposes.

WINIGER & LUDWIG (1974) developed a device for measuring these. While RUDORF & BAERECKE (1958) in their experiments found flat eyes to be dominant, HOWARD (1978) observed the opposite in other parent combinations. A parent with deep eyes shifts the progeny in the direction of deeper eyes in most cases. The preference for a distinct flesh colour, ranking from white to deep yellow for potatoes to be consumed fresh, varies from

Tab. 18: Requirements for potatoes intended for processing
Anforderungen an Kartoffeln zur Herstellung von Fertigprodukten (KELLER und BAUMGARTNER 1982)

trait *Merkmal*	french fries *Pommes frites*	crisps *Chips*	mashed potatoes *Speiseflocken*	canned potatoes *Dosenkartoffeln*
tuber form *Knollenform*	regular oval flat eyes *regelmäßig, oval, flache Augen*	round or oval *rund bis oval*	round or oval *rund bis oval*	round or oval, flat eyes *rund bis oval, flache Augen*
size *Knollengröße*	42.5–70 mm	42.5–70 mm	as required by the manufacturer *wie vom Hersteller verlangt*	below 35 mm *unter 35 mm*
starch content	14–16 %	15–18 %	15–19 %	12–14 %
cooking type *Kochtyp*	B EV, B–C	B–C or C	B–C or D–C easy disintegration during steaming *lockeres Zerfallen beim Dämpfen*	B–A or A
darkening after cooking *Kochdunkelung*	low *gering*	low *gering*	low *gering*	very low *sehr gering*
susceptibility to blue spot *Blauempfindlichkeit*	low *niedrig*	low *niedrig*	low *niedrig*	low *niedrig*
darkening in raw state *Rohverfärbung*	medium *mittel*	–	low *niedrig*	medium *mittel*
content of reducing sugars *Gehalt an reduzierenden Zuckern*	not much more than 0.5 % of fresh matter *nicht wesentlich mehr als 0,5 % der Frischsubstanz*	not much more than 0.5 % of fresh matter *nicht wesentlich mehr als 0,5 % der Frischsubstanz*	up to 1 % of fresh matter *bis 1 % der Frischsubstanz*	up to 1 % of fresh matter *bis 1 % der Frischsubstanz*
susceptibility to mechanical damage *Schlagempfindlichkeit*	low *niedrig*	low *niedrig*	low *niedrig*	low *niedrig*

country to country, whilst for processed products the flesh colour of the cv. is usually without importance. Yellow colour is dominant over white (HOWARD 1970, WINIGER & LUDWIG 1974). Intermediates are controlled by minor genes (HOWARD 1978). Greening of the tubers has gained in importance with the demand for washed and pre-packed potatoes. Light exposure, moreover, favours the formation of glycoalkaloids (see below). The tendency towards discolouration is not desirable for raw tuber material or for cooked tubers. It results in raw tubers from oxidation of tyrosine and chlorogenic acid by the action of polyphenoloxydases. It involves the development of dark coloured melanines and other compounds (GRAY & HUGHES 1978, MÜLLER 1979). UMAERUS & OLSSON (1974) found a significant high correlation between tyrosine content and the intensity of discolouration of raw potato mash after two hours. VOGEL (1966) estimates the discolouration by means of a

Aardevo Exhibit 1013
Page 0099

Tab. 19: Charakteristics of types of cooked potatoes
Beurteilung der Speisekartoffeltypen (KELLER und BAUMGARTNER 1982, modified)

	A: salad potato (firm) *Salatkartoffel (fest)*	B: usable for all purposes *für alle Zwecke verwendbar*	C: mealy potato *mehlige Kartoffel*	D: very mealy potato *sehr mehlige Kartoffel*
disintegration in cooking *Zerkochen*	remaining whole *ganz bleibend*	slightly fallen *wenig aufspringend*	badly fallen *stark aufspringend*	completely disintegrated *vollständig zerfallend*
consistency of flesh *Textur*	*firm* *fest*	moderately firm *mäßig fest*	fairly soft *ziemlich weich*	soft with variable consistency *weich mit ungleicher Konsistenz*
mealiness *Mehligkeit*	not mealy *nicht mehlig*	slightly mealy *schwach mehlig*	mealy *mehlig*	very mealy *sehr mehlig*
moistness *Feuchtigkeit*	moist *feucht*	slightly moist *wenig feucht*	fairly dry *ziemlich trocken*	dry *trocken*
structure of the starch grain *Struktur des Stärkekorns*	fine *fein*	fairly fine *ziemlich fein*	fairly coarse *ziemlich grob*	coarse *grob*
colour[1] *Farbe*	W 1 = pure white – *rein weiß;* W 2 = gray white – *grauweiß;* W 3 = yellowish white – *gelblich-weiß* G 1 = pale yellow – *hellgelb*; G 2 = yellow – *gelb;* G 3 = deep yellow – *tiefgelb*			
taste *Geschmack*	without – *ohne*; faint – *schwach;* strong – *kräftig;* very strong – *sehr kräftig*			

[1] according to the preference in the country
je nach der Benutzung im jeweiligen Land

chromatographic paper strip dipped into the sap of raw tubers, and after drying determines the colour with a leucometer. PAPENHAGEN & MÖLLER (1978) incubate cylinders of tuber flesh of 4 mm diameter at 18–20 °C for 4–48 hrs and score the course of discolouration visually. Colour tables are in use as well. The high influence of environmental factors makes it necessary to pursue the observations over several years. Interestingly, several wild species withstand discolouration of raw tuber flesh, in particular *S. hjertingii* (FIRBAS 1961, WOODWARD & JACKSON 1985).

Potatoes for cooking have been classified into four types as a result of consultations by the section »Breeding and varietal assessment« of the EAPR *(Tab. 19)*. The first three enumerated traits, i. e. disintegration, consistency (= texture) and mealiness are related to the starch content and to the separation of the cells in the course of cooking. Also important for the consistency and the moisture is the protein and the relation of protein to starch. HOLDEN (1981) often found a strong positive correlation between disintegration, mealiness and dry matter content.

Flavour is a very complex property comprising a lot of physical and chemical components (LINEHAN & HUGHES 1969, WINIGER & LUDWIG 1974). BURI et al. (1970) believe that free amino acids and free nucleotides are essential for the flavour. Not unimportant for the taste are volatile substances. Statements of cooking quality cannot dispense with organoleptic screening (BOEHLER et al. 1984). Data from single cvs. or breeding material over several years and from many replications in different regions must be collected before a final picture can emerge. MÖLLER & VOGEL (1961), studying the inheritance of mealiness, found large

Aardevo Exhibit 1013
Page 0100

differences in four progenies ranking from 4 % of non-mealy clones in the one progeny up to 100 % in another. It is astonishing, that the flavour remains fairly stable in the face of changing environmental factors (NEENAN et al. 1967).

Discolouration after cooking results from the formation of complex compounds of chlorogenic acid and iron ions. The presence of citric acid and other acids retards the formation of the complex (GRAY & HUGHES 1978, MÜLLER 1979). The discolouration is measured visually by comparison with colour tables. The negative influence of some types of soil, particularly heavy ones, is great. Inheritance studies of chlorogenic acid were performed by UMAERUS & OLSSON (1974). DALIANIS et al. (1966) found that selection for non-blackening early in a breeding programme is effective. Differences in the progenies are less pronounced (MÖLLER & VOGEL 1961). A planned combination of the single components of internal quality and flavour seems impossible, because of the small chance of obtaining a seedling which possesses not only the abovementioned traits but also a high yield potential and an acceptable resistance to so many diseases. Therefore, most potato breeding programmes follow the practice for complex characters, combining only genotypes with fair expression of the traits in both parents and avoiding bad ones. It is possible to increase considerably the share of good tasting clones in the progenies in this way (SCHEIDT & HUNNIUS 1978).

Starch and dry matter content are correlated (SIMMONDS 1977). Deviations are attributed to varietal differences of the spaces between the cells (WINIGER & LUDWIG 1974, NISSEN 1967). Starch and dry matter content are determined by measuring the weight under water. Another method, particularly applied to seedling population, is the floating of tubers in salt solutions of different concentrations (MÖLLER 1965).

High starch content is connected with late maturing in most cases. MUNZERT & SCHEIDT (1978) stated a positive correlation with $r = 0.51^{++}$. MARIS (1969) founds no significant correlation. It is possible, however, to produce early genotypes by combination of suitable parents with about 20 % starch (MÖLLER 1965). High starch content and high yield were found to be negatively correlated (HUNNIUS 1969 a, MARIS 1969, SCHEIDT & MUNZERT 1985), or not to be correlated ($r = 0.03$, MUNZERT & SCHEIDT 1978). It is possible to improve the combination of high starch content with high yield, when the starch content of both parents does not drop below a certain limit.

Cvs. with highest starch yield among the earlies and medium earlies in the Federal Republic of Germany are cvs. Katja, Kero, Roeslau, Tella and Ute, and among the medium late and late ones, cvs. Indira, Pirola, Pruceres and Ragna. Primitive cultivated and wild species and their back-cross hybrids, are generally high in starch. RUTTENCUTTER et al. (1979) found that dihaploids based on the cultivated diploid species *S. phureja* and *S. stenotomum* transmit high starch content in 4x · 2x-crosses, while SCHEIDT & MUNZERT (1985) point to the high starch content and yield in *S. stoloniferum* back-cross lines.

A low level of reducing sugars is an important criterion of quality for most processed products as mentioned above. Not only the actual content at the time of harvest is important, but also the course of its increase during long storage. Storage at $\leqq 8$ °C leads to a higher content. Therefore, higher temperatures are applied in order to reduce it, while the onset of germination is retarded by chemical sprout suppressants. Higher contents, can also be reduced by re-conditioning, i. e. by applying a temperature of about 20 °C for 2–3 weeks before processing. Several chemical and, particularly, enzymatic methods are available for the determination of reducing sugars (WINIGER & LUDWIG 1974). Rapid techniques for selection purposes are the tes-tape test and the mini-bake trial by means of a special kit. A good positive correlation exists between content of reducing sugars and dark colouration of the chips. But there is only a low one between content of reducing sugars and dry matter (PUTZ et al. 1982).

All the traits important for processing, such as content of reducing sugars, its increase at temperatures between 6 °C and 8 °C, its increase up to the beginning of July, and the response to re-conditioning, are under separate genetic control in the single cvs. (STRICKER,

Aardevo Exhibit 1013
Page 0101

HUNNIUS, SCHILLING & MUNZERT, unpubl.). It should be mentioned that BRIGHT et al. (1984) found somaclones of cv. Record with low sugar content (Section 5.2.2.2).

ACCATINO et al. (1973) found two dominant genes responsible for re-conditioning ability. At least one of the genes must be present when darkening is to be blocked. The mini-bake trial is also applicable for testing of fresh and deep-frozen chips. The question as whether or not varieties with special suitability for processing should be bred is answered negatively by most authors. The spectrum of cvs. is evidently broad enough (ADLER & STRICKER 1977, HUNNIUS 1981, PUTZ et al. 1982, PUTZ & KEMPF 1983).

The protein question needs some introductory remarks. The high value of potato protein has already been mentioned (Section 1 and 9.1; *Tab. 2*). The protein content of the present varieties is comparatively low, but more than one third of the human protein requirement of people im Europe and North America is provided by the daily potato dish (BURTON 1974). Because other protein sources are abundant used, there seems no necessity to increase the content in cvs. destined for the developed countries. Quite different is the situation in the Third World where the lack of protein in the diet is an ever increasing problem and a prominent breeding goal for the future. If in several developing countries the potato is at present still an occasional and not inexpensive addition to the meal it has all the potentialities of becoming a cheap staple food in many developing countries in the future, provided suitable economic and agricultural conditions are established in the course of developmental aid (SAWYER 1984).

A strong relationship between starch and protein was found by HUNNIUS et al. (1973). Cvs. rich in starch show a high protein level as well. The relation between protein and processing ability is not clear. However, most cvs. preferred by the processing industry have an above average protein content. Several methods for assessing the protein have been developed (STEGEMANN et al. 1973, HUNNIUS et al. 1973, WINIGER & LUDWIG 1974, KLING & SCHMÜTZ 1977). Crude protein consists of 50 % true protein and 50 % non-protein N. There is no correlation between crude protein content and maturity classes, but a high positive one with dry matter content (MÖLLER 1965, MUNZERT & SCHEIDT 1978). A slight negative correlation exists with tuber yield. The combination of higher protein content with average tuber yield seems nevertheless possible (MÖLLER 1965, DESBOROUGH & WEISER 1972, MIEDEMA et al. 1976). MÖLLER (1965) believes that the variation among the cv. assortment is sufficient for increasing the protein content by breeding. DESBOROUGH & LAUER (1977) doubled the protein content by using *S. phureja* in 4x · 2x-crosses (see also VEILLEUX et al. 1981). 40 % of the tuber protein has a molecular weight of 40,000 and is represented by a single protein species called patatin or tuberin (PARK 1983). It is intended to isolate and transfer the responsible gene in order to increase the protein formation (WILLMITZER, pers. comm.).

The leaves and tubers of the potato contain a number of different glycoalkaloids as normal constituents. Their aglucons belong to the class of steroids. Those carrying a double bond in the aglucon cause a burning and bitter taste when present above a certain concentration level. In still higher concentrations the glycoalkaloids are poisonous for both man and animal.

In earlier years attempts were made to transmit glycoalkaloids from *S. chacoense* into the leaves of cvs. in order to protect them from the Colorado beetle (SCHWARZE 1963). Today the glycoalkaloids of the tuber are of more interest to the breeder for reasons of flavour. Genuine for *S. tuberosum* are mainly α- and β-solanine, α- and β-chaconine and leptine. They all carry a double bond in the aglucon and therefore influence the taste negatively. The glycoalkaloid demissine (without a double bond) was introduced into many cvs. by hybridization of their progenitors with *S. demissum* (Section 2.5). Other glycoalkaloids possibly introduced from other wild species may also be present as traces (*Tab. 4;* GREGORY 1984).

Statements about the glycoalkaloid content and the level beyond which the flavor is influenced differ with the method used. Gravimetric as well as colorimetric ones are elaborated. SANFORD & SINDEN (1972) with their method of TGA- (total glycoalkaloid

Aardevo Exhibit 1013
Page 0102

content) determination found in 19 cvs. and parental lines (except one escape) mean values of TGA between 3.6 and 14.5 mg per 100 g fresh weight in two years' experiments. SINDEN & WEBB (1972) found a range between 1.4 and 39 mg in five cvs. at 39 sites in two years. ROSS et al. (1978) applying the method of SCHWARZE (1963) to analyse the glycoalkaloids with a double bond, found in 35 cvs. at five sites and in five years mean values between 0.73 and 5.25 mg, while single tubers contained up to 10 mg.

The intensity of the burning and bitter sensation was highly correlated with TGA content. Contents beyond 14 mg were rated as bitter (SINDEN et al. 1984). Taste analyses carried out by Ross et al. (1978) with a panel of five people showed that the score »bad« or »burning« stated by at least two members of the panel began with 10 mg. Studying the usual environmental influences in glycoalkaloid content, the authors found a variation of up to 78 % over five years and of up to 50 % in three localities. Tubers exposed after harvest to daylight for 11 weeks and having turned green showed an up to fourfold increase in the values. However, cvs. also exist with only 0.7 fold increase.

Most wild species, such as *S. chacoense, S. demissum,* etc. contain high levels of TGA. Inheritance studies made by PROKOSHEV et al. (1952), ROSS (1966) and SANFORD & SINDEN (1972) lead to the following conclusions. The differences in TGA content of wild species and *S. tuberosum* are governed by major and minor genes. Dominant (?) genotypes are discarded by flavour tests in subsequent back-cross families. Therefore, a low and medium TGA content prevails in cvs. and the usual parental material. The TGA-values from offspring of such intermated back-cross parents come close to the mid-parent values and show a fairly continuous variation with some escapes to higher concentrations. ROSS et al. (1978) could show that there is no difference between pure ssp. *tuberosum* and wild species based cvs. either in their glycoalkaloid content or in the taste. A well known example is that of cv. Lenape (B 5141-6). Lenape possesses genes from *S. chacoense* and contains 15.4–35.4 mg glycoalkaloids (ZITNAK & JOHNSTON 1970). It was nevertheless a parent of cvs. Atlantic, Belchip, Russette, Seminole and Simcoe and a grandparent of Islander and Yankee Chipper. These all evidently contain ordinary levels of glykoalkaloids.

It is difficult to say whether or not chemical tests of TGA should be recommended for general application in breeding. Smaller units with early applied organoleptic tests may dispense with it.

The potato is considered an important source for maintaining the necessary level of vitamin C. The content varies between 13.2 and 54.1 with cv. and storage time (THORNTON & SIECZKA 1980). Increasing the ascorbic acid content is an important breeding aim for cvs. used in developing countries whilst the need in developed countries is covered by other cheap sources e. g. fruit. Wild species with higher ascorbic acid content are available (SINDEN et al. 1978).

In quality characters a medium expression in so many traits as possible should be aimed at. Moreover, high stability which is a favorite breeding aim (HOLDEN 1981), and has been established as a criterion for the classification of cvs. (KRÄTZIG 1980), is more easily to combine with medium expression than with a pronounced one. A high stability in quality is attributed to following German cvs.: Aula, Berolina, Christa, Clivia, Forelle, Grata, Hansa, Isabel, Jessica, Nicola, Pinki and Prima.

Aardevo Exhibit 1013
Page 0103

10 Production of seed potatoes

Seed production aims at providing tubers for the grower as free of pathogens as possible. New developments in sterile multiplication and virus assay have lead to several fundamental improvements.

Three methods are now in use. With the classical method only mother plants are grown in the greenhouse, further propagation taking place outdoors (WRIEDT 1977, HUNNIUS 1977 a). The mother tuber and the plants grown from it (pre-A-clones) as well as the initial stocks must be intensively indexed for freedom from viruses. A-, B-, C-clones, and still more propagation steps follow yearly until certified seed, the last propagation step, is sold to the grower. The last categories are supervised and controlled by official agencies. Official directives regulate dates for the application of aphidicides, and later on of herbicides for haulm destruction to prevent late virus infections from migrating into the tubers. Rules also regulate the permissable percentage of virus infections at the different yearly propagation steps from basic or foundation seed (S, SE, E) to certified seed (A, B, C) (HIDDEMA 1972). The system is modified in different countries and climatic regions. Seed production can only be performed in areas where aphid infestation is low. Breaking of tuber dormancy causes the plants quickly to enter a stage of age-resistance to virus infection. Chemical weed-killers are applied instead of machines to avoid virus spread by contamination. A simple latex kit suited for on-site testing is strongly recommended for inspection of the plants (TALLEY et al. 1980). It works without a microscope. Diseased plants are rogued out.

A method of stem-cuttings propagation was first introduced by JACOBSEN (1973) in Denmark and J. L. HARDIE in Scotland, see further HUNNIUS (1977 a) and HAMANN et al. (1979). Stock plants thoroughly tested for freedom from viral, bacterial and fungal infects are dissected into leafed stem-cuts with axillary buds and grown in soil in the greenhouse under steady sanitary control. Starting with two tubers and plants, 18.000 tubers can be collected after 10 months multiplication. This method, moreover, under certain circumstances reduces blackleg infections (GRAHAM et al. 1976, PÉROMBELON et al. 1980, MASTENBROEK & BAKKER 1984). This method can be improved considerably by starting with plantlets from sterile meristem cultures (WRIEDT 1984). The plantlets are propagated in greenhouse in soil.

The third and most promising method is the complete sterile micropropagation (FOLDØ 1983). It starts with the culture of a few mm meristem tips on agar medium, often sustained by thermotherapy and virazole (CASSELS & LONG 1982). Absolutely virus-free plantlets and tuberlets can be obtained by this method (MELLOR & STACE-SMITH 1977, ROCA et al. 1978, GOODWIN et al. 1980, BRYAN et al. 1981, FOLDØ 1983, SCHILDE-RENTSCHLER et al. 1984). Eradication of PSTV is possible, as well, when low temperature is applied to meristem culture (LIZARRAGA et al. 1980).

The sterile plantlets are cultivated in vitro in a sterile greenhouse. They are multiplied by single-nodes during several vegetative generations until to the end of the year. Finally transplants or tubers are produced for planting in the field *(Fig. 21)* where, as it is recommended, they should be held in a gaze-greenhouse in the first year to protect them against aphids.

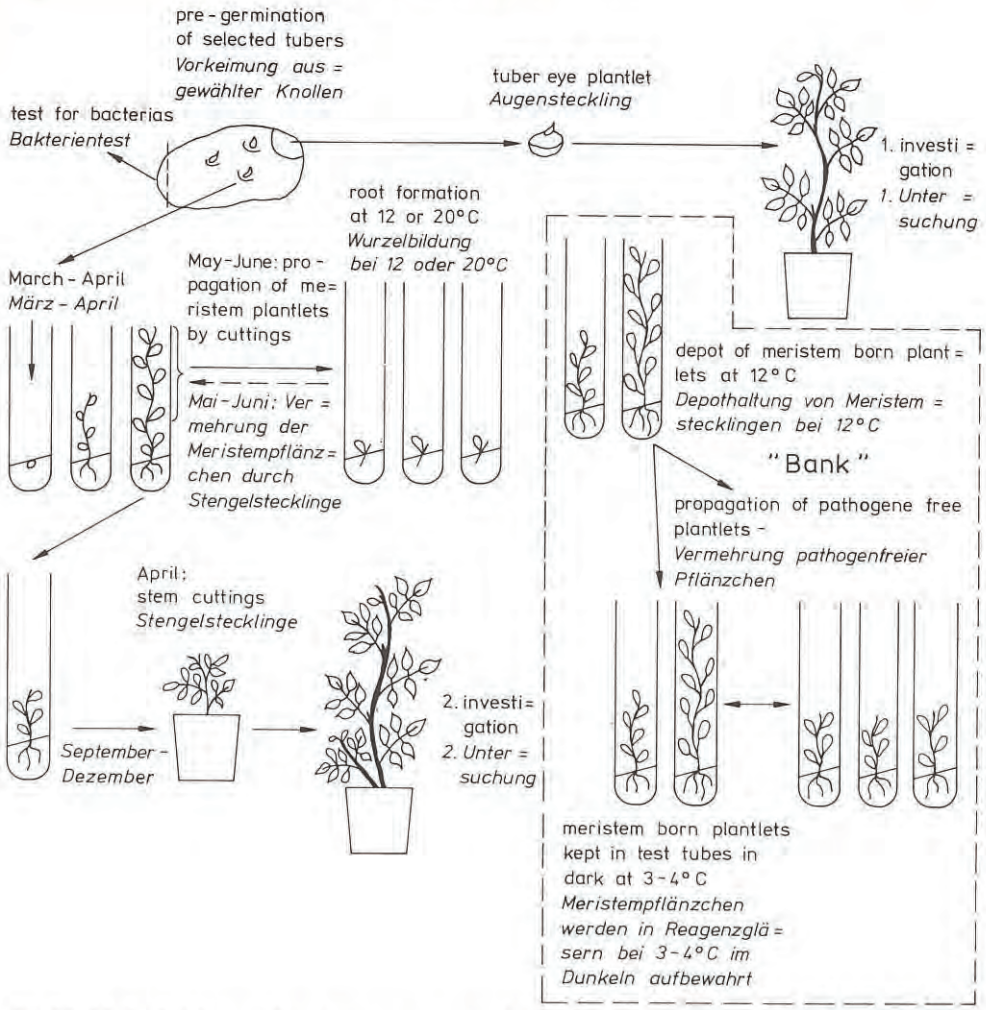


Fig. 21: Method of fast sterile micropropagation at the start of clone propagation and seed production *Methode der schnellen, sterilen Mikrovermehrung bei der Klonenvermehrung und Saatgutproduktion* (FOLDØ 1983)

Complete sterile micropropagation has three main advantages:

1. Freedom from viruses of the cuttings prepared for planting in the field;
2. saving of 2–3 years of exposure to field pathogens;
3. strong reduction of infections with *Erwinia carotovora* and *Corynebacterium sepedonicum.*

Whether or not the CSM method is superior to the less costly incomplete one depends from the special situation of the seed production unit. Complete sterile micropropagation is already obligatory in Danmark and Scotland and performed in The Netherlands. Plantlets of many cvs. are available in governmental institutions, such as the Netherland-German Potato Genebank, Brunswick (MIX 1981) and the International Potato Center, Lima (SCHILDE-RENTSCHLER et al. 1983, 1984).

Aardevo Exhibit 1013
Page 0105

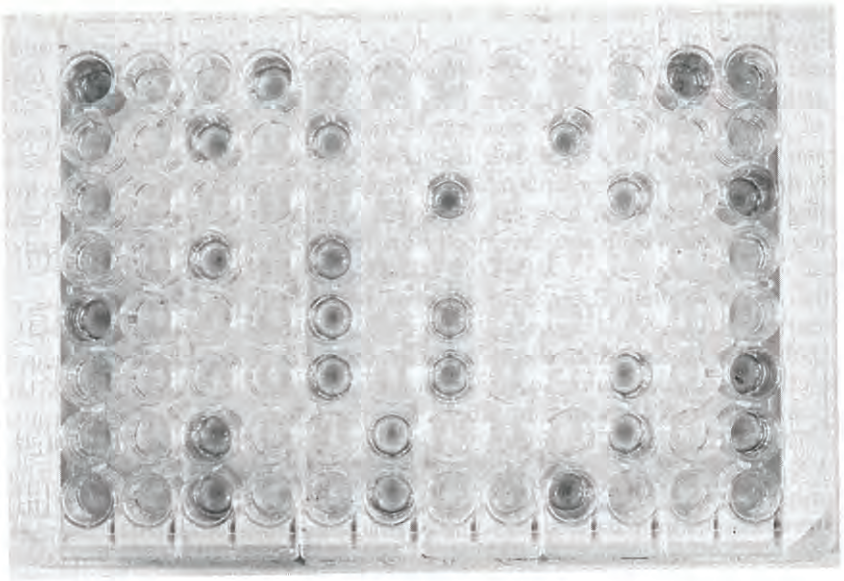


Fig. 22: ELISA test plate with cavities for 96 tests. Dark cavities mark presence of virus, clear no virus
ELISA-Testplatte mit Vertiefungen für 96 Proben. Die dunkel gefärbten Vertiefungen zeigen Virusgegenwart, die ungefärbten Virusfreiheit der Probe an (by courtesy of H. UHRIG)

Several methods are used for virus diagnosis during seed production (DE BOKX 1972 a, HUNNIUS 1977 b): visual inspection of tuber eye index plants in winter time, sap transmission to indicator plants and particularly for PVA, PVX and PVY to cut leaves of A 6 plants, i. e. a hybrid of *S. demissum* and Aquila. Microscopic inspection of excessive callose in sieve tubes was extensively used to detect PLRV infections. Routine serological precipitation tests of all viruses, except PLRV and the viroid PSTV, was also formerly common practice. Practically all these methods have now been replaced by a new serological method: the enzyme linked immunosorbent assay (ELISA; WIGGER 1983, VETTEN et al. 1983, EHLERS & PAUL 1984, GRIMM & DANIEL 1984, GUGERLI 1985).

The new method consists of four steps and multiplies the usual antibody-virus effect: 1. polystyrol test plates with small cavities are coated with virus specific antibodies; 2. the antibodies react with virus particles of raw or clarified plant sap to form a complex fixed on the wall; 3. specific enzyme labelled antibodies are then added which react with the antigens; 4. the enzyme reacts with an added substrate to release a coloured compound *(Fig. 22)*.

The intensity of the colour then measured is related to the virus content of the plant sap. Several kits have been developed allowing more than 1000 test per day. Sensitivity can be improved by using monoclonal antibodies. They are obtained by a specific preparation and have many advantages. They react with common antigenic determinants of many different strains, thus overcoming the more or less strict strain specificity of the usual polyclonal antibodies (KÖNIG 1981). With ELISA the problems with the detection of PVA, PVM, PVS, PVX, PVY, TRV and PLRV in plants, index plantlets or plantlets from tissue cultures seem to have been solved. However, the detection of some viruses, particularly of the leaf roll virus in tubers, even after breaking dormancy is at present still unsatisfactory. PSTV cannot be identified by ELISA or other serological methods, because it lacks the protein coat. However, its assay is possible by the autoradiographic dot-blot test. This very sensitive new method, based on molecular hybridization (complementary DNA, cDNA) can perhaps also be used for any virus and perhaps may play an important role in virus identification as well as

Aardevo Exhibit 1013
Page 0106

in routine virus testing particularly for the detection of the viroid PSTV (SALAZAR et al. 1983, FLAVELL et al. 1983). However, the cDNA method needs very special and costly equipment and installations because radio-active substances are involved. For each viral RNA, radioactive copies of complementary DNA are prepared by means of plasmids. Drops of raw or clarified sap or macerated true seeds are placed on a nitrocellulose membrane, then incubated with ^{32}P-labelled cDNA, washed out and finally clamped next to an X-ray film. Sap drops from virus-infected plants show up as dark spots on the film after developing 80–150 plants per hour can be tested, but altogether four days are needed for preparation. There has been also developed a method which combines ELISA- and cDNA-technique.

Another sensitive method for routine testing is the antibody sensitized latex method (QUERFURTH & PAUL 1979, TORRANCE & JONES 1981, FRIBOURG & NAKASHIMA 1984). Latex are tiny polysterol spheres which absorb antibody molecules. The test is simpler than ELISA and the cDNA test. It requires less expenditure on apparatus. PVS and PVX, at least, already can be detected in dormant tubers. But the test seems to be less sensitive than ELISA. The International Potato Center, Lima, has available sensitized latex antisera of PVS, PVX, PVY and two Andean viruses for distribution. This method is also suitable as an assay for bacteria such as *Corynebacterium sepedonicum* (SLACK et al. 1979).

Seed production, as can be seen, has developed into a very complicated and sophisticated matter and has become an industry in itself in developed countries. It must be stated here that this system cannot be transplanted to every developing country. There are, however, two other ways, apart from the production of special virus free tuber seed, to promote potato cultivation in the Third world. One is the culture of true seed potato (Section 6), and the other, the growth of highly virus-resistant cvs. which do not need sophisticated seed production techniques. Cvs. »immune« to all viruses are not available. However, cvs. with »immunity« or localized hypersensitivity to PVA, PVM, PVS, PVX and PVY do exist (Section 6.2). Breeding of cvs. with near »immunity« to PLRV is under way. This success will be of benefit to the farmer when »immune« or very resistant cvs. adapted to special regions are bred, and when simple sanitary techniques are developed which can be handled by the farmer on his farm. This relieves the low income grower of major reliance on seed importation.

Aardevo Exhibit 1013
Page 0107

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Aardevo Exhibit 1013
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Aardevo Exhibit 1013
Page 0111

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Aardevo Exhibit 1013
Page 0112

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Aardevo Exhibit 1013
Page 0113

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Aardevo Exhibit 1013
Page 0114

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Aardevo Exhibit 1013
Page 0115

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Aardevo Exhibit 1013
Page 0116

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Aardevo Exhibit 1013
Page 0117

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Aardevo Exhibit 1013
Page 0118

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Aardevo Exhibit 1013
Page 0119

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Aardevo Exhibit 1013
Page 0120

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Aardevo Exhibit 1013
Page 0121

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Aardevo Exhibit 1013
Page 0122

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Aardevo Exhibit 1013
Page 0123

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Aardevo Exhibit 1013
Page 0124

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Page 0125

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Aardevo Exhibit 1013
Page 0126

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Aardevo Exhibit 1013
Page 0127

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Aardevo Exhibit 1013
Page 0128

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Aardevo Exhibit 1013
Page 0129

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Aardevo Exhibit 1013
Page 0130

Subject Index

acronecrosis 73
adaptability 10
Agrobacterium 58–60
Agropyrum 57
allosyndesis 24
Alternari 52
analytical breeding 32–34, 46, 47, 86
analytic-synthetical breeding 32, 46, 49
androgenesis 31, 35, 46, 47
anther culture 46–49
anthozyanine 34
aphidicides 69, 70, 103
aphids 66, 68–70, 73, 103
apomixis 62, 63
asymmetric hybridisation
autotetraploid 10, 24, 25
AVF 68

B*acillus thuringiensis* 60
Bacterium solani 64
bean 59
black leg 94, 103
black scurf 89
black spot, blue spot, bruising 90–92, 98
BWYV 70

callus 36, 37, 49, 50, 51–53, 56, 85
Capsella 70
cDNA 105, 106
chaconine 83
chimaerism 36, 37, 53, 59
chlorogenic acid 100
chondriome 55–57
chromatid and chromosome segregation 24
CMS 22, 23, 56–58
colchizine treatment 32, 33, 36, 37, 49, 62
Colorado beetle 12
combining ability 25, 27, 30
cooking type 29, 99
Corynebacterium 16, 62, 104
crisps 29
crown gall 58, 59
cryopreservation 21
cultivated species 14–21
cuttings 56
cybrids 23

damage drum 91
Datura 55, 57
day length 15, 29
deamplification 54
decapitation 27, 35
desynapsis 40
dihaploids 16, 26, 27, 31–38, 42, 44, 46–48, 55, 89
dikaryon 54
diplogamates 32, 37–39, 42
discoloration 29, 92, 98, 100
dry matter 100, 101
dry rot 64, 92
duplex 24

EAA 9, 97
EBN 23
Eisenfleckigkeit 74
electrofusion 57
electroporation 60
ELIZA-test 67, 70, 71, 74, 105
Empoasca 12
embryo spot 34, 42
endomitosis 37
endosperm 16, 23, 34
energy production 9
epistasis 25
Erwinia 60, 62, 90, 92, 93, 104
expeditions 21, 50
explants 36
eye depth 28, 29

FDR 16, 32, 37, 40–45
fertility 22, 36, 37, 39, 54, 44
flavour 99, 100
flesh colour 28, 29, 35, 97, 98
food production 10
foundation seed 50
french fries 29
frost 10, 12, 52
Fusarium 12, 13, 52, 65, 66, 90, 92, 94
fusion 21, 23, 31, 36, 56, 58

gametes, unreduced 23, 32, 33, 37, 38, 49, 63
gangrene 92
gene amplification 49, 53
genebank 21, 50
gene expressivity 38, 42
gene-for-gene system 78, 83
gene interaction 25, 26, 32, 34, 46
gene resource 94
gene transfer 58, 59, 63, 66, 68, 84
germ plasm 21
Globodera 12, 13, 20, 45, 47, 52, 73, 75–82
glycoalkaloids 98, 101, 102
Gomphrena 73
Gynogenesis 46, 47

haploids 34
Helminthosporium 53
heritability 24, 35
heteroallelism 10, 25, 26, 57
heterosis 15, 25–27, 32, 36, 39, 45
homodiploid 46
homo- and heterofusion 54
hypersensitivity 64–93

inbreeding 25, 33, 35, 62
incompatibility 22, 54, 84
incongruity 22
indicator plants 27
Internacional Potato Center (CIP) 10, 30, 82, 104

inter-dihaploids 16, 33, 35, 46, 48, 57, 62
intolerance 65, 69
IVR 68

kanamycin 59

late blight 12, 13, 19, 24, 30, 35, 64
latency 70
latex method 103, 106
Lycopersicon 56, 73

maize 9, 59
maturity 24, 28, 29, 90, 91, 95, 96, 101
meiotic doubling 31, 33, 36, 37, 38, 46, 62, 66
meristem 36, 37, 50, 103
micromanipulator 55
micropipette 55
micropropagation 103, 104
microspore 48, 49
mitochondria 13, 55, 56, 62
monohaploid 26, 31, 32, 34, 46, 47, 49, 58
mitotic doubling
mutation 50, 53, 54
Myzus 68, 70

nematodes 12, 13, 21, 24, 29, 30, 35, 36, 38, 59, 66, 73, 75–82
Neo-Tuberosum 19, 30
Netherland-German Potato Genebank 104
Nicotiana 53, 54
non-blackening 100
non-host resistance 57, 58

opines 58
overdominance 25

parasexual 54
Paratrichodorus 75
parthenogenesis 31, 34, 46
parthenote 34, 42
pathosystem 66
pedigree breeding 30
penetrometer 91
pentaploid 16
Petunia 82
phaseolin 59
pheromone 13, 68
Phoma 53, 65, 90, 92, 93
Phthorimaea 13
Physalis 55, 82
phytoalexin 52, 83, 84, 93
Phytophthora 45, 52, 57, 62, 82–86
phytotoxin 52
plasmid 23, 55–62, 66, 106
plasmon 19, 22, 23, 53, 55, 57, 58
plastid 23, 54, 55
plastom 55, 56
ploidy crossing 31
PLRV 12, 13, 24, 35, 47, 49, 51, 52, 57, 64–74, 105, 106
pollen 28, 30, 39, 40, 42, 47, 49, 62
pomatoes 56
pommes frites 29, 95
population breeding 30
processing 10, 97, 98, 101
protein 9, 13, 24, 97, 101
protoclones 50, 52, 53, 56
pseudogamie 31, 32, 34
Pseudomonas 13
PSTV 62, 64, 75, 105, 106
pubescence 13, 68
PVA 12, 19, 47, 65, 66, 69, 74, 105, 106
PVM 64, 65, 66, 69, 73, 105, 106
PVS 57, 65, 66, 69, 74, 105, 106
PVX 19, 24, 35, 36, 41, 47, 49, 65–68, 72, 73, 80, 105, 106
PVY 12, 22, 24, 30, 35, 47, 49, 52, 64–72, 74, 80, 105

quadrigametic tetraploids 37, 39, 43, 44, 46

rebound pendulum 91
re-conditioning 100, 101
reducing sugars 12, 13, 97, 98, 100
regeneration 48–50, 54, 60
resistance, agronomic 81
resistance, extreme 64–73
resistance, field 64–93
resistance, horizontal 64
resistance, vertical 64
resistance to infection 64–93
reziprocal differences 24, 56, 84
Rhizoctonia 62, 69

S-alleles 22, 35
scab 19, 28–30, 35, 52, 88
Scopolia 75
SDR 37, 39–41, 43
Secale 57
seed tuber production 103–106
soft rot 93, 94
solanines 83, 101
Solanum acaule 12, 14, 16, 17, 20, 22–26, 36, 53, 65, 69, 70, 72, 73, 75, 88
– x *ajanhuiri* 14
– *andigena* 14, 15, 19, 21, 26, 30, 42–44, 61, 65, 69, 72, 74, 77–80, 86, 88
– *ballsii* 79
– x *berthaultii* 13, 75, 86, 87
– *brevidens* 16, 50, 51, 57, 70
– *bulbocastanum* 13, 16, 22, 82, 86
– *canasense* 18
– *capsicibaccatum* 13
– *cardiophyllum* 23
– *chacoense* 11, 16–23, 35, 56, 71, 86, 101, 102
– x *chaucha* 14, 15
– *chiquidenum* 86
– *circaeifolium* 86
– *commersonii* 12, 13, 17, 18, 20
– x *curtilobum* 14, 16
– *demissum* 12, 13, 17, 19–23, 50, 53, 69, 71, 72, 82–86, 101, 102, 105
– x *edinense* 19, 20
– *etuberosum* 13, 16, 50, 51, 70, 86
– *famatinae* 12, 81
– *fendleri* 13, 18, 20, 86
– *fernandezianum* 51
– *gourlayi* 13, 35, 65, 74, 81, 86
– *guerreroense* 75
– *hjertingii* 13, 86, 99
– x *juzepczukii* 14, 15, 26
– *kurtzianum* 13, 21, 77
– *leptophyes* 18
– *lignicaule* 82
– *(Longipedicellata)* 12
– *maglia* 13, 17, 18, 20, 22
– *megistacrolobum* 14, 38, 74, 82
– *microdontum* 13, 17, 20, 21, 33, 71, 74, 86
– *multidissectum* 86
– *multiinterruptum* 77, 78, 86
– *nigrum* 56
– *oplocense* 36, 81
– *papita* 86
– *pennelli* 50
– *phureja* 12, 14, 16–26, 30, 34–36, 38, 42–47, 57, 58, 65, 70, 71, 86, 100, 101
– *pinnatisectum* 13, 16, 70, 86
– *polyadenium* 22, 82, 86
– *polytrichon* 16, 47, 86
– *quimense* 86
– *raphanifolium* 70
– *rybinii* 14

Aardevo Exhibit 1013
Page 0132

– *simplicifolium* 21
– *sparsipilum* 13, 14, 17, 18, 35, 38, 81
– *spegazzinii* 12, 17, 20, 23, 24, 35, 38, 72, 79–81
– *stenotomum* 14, 15, 18, 20, 25, 26, 30, 35, 43, 57, 70, 71, 100
– *stoloniferum* 12, 13, 16, 17, 20, 22, 24, 28, 29, 36, 53, 62, 65, 71–73, 81, 82, 86, 90, 100
– *suaveolens* 82
– *sucrense* 65, 73
– *toralapanum* 13, 21
– *vernei* 13, 17, 20, 22, 23, 35, 38, 73, 77, 82, 85, 86
– *verrucosum* 13, 16–19, 22, 70, 82, 85, 86
somaclones 21, 32, 49–54, 57, 69, 72
somatic hybridisation 21, 36, 46, 47, 66
spraying 74
sterility 22, 23, 46, 47
starch 13, 24, 28, 29, 91, 97–101
sunflower 59
synkaryon 54
Synchytrium 13, 87

taste 98
tetraallelism 10, 24, 25, 26, 31, 46
tobacco 58, 59
tetrad sterility 22, 62
texture 91, 99
tolerance 38, 66, 67, 96
tomato 75
topatoes 56
transformation 58
transgression 43, 64
transplants 61
transposons 53
Trichodorus 75
triploid 16, 34, 38, 39
Triticum 59
true seed potato (TIPS) 21, 57, 61–63, 106
TRV 65, 66, 74, 75
tuber damage 90–98
tuber indexing 69
tuber moth 12
tuber shape 28, 29, 96

viroid 75
vitamin C 102

wart 11, 19, 29, 30, 35, 87, 88
wheat 58
wide hybridisation 26, 46
wild species 11–21, 32

zein 59