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Julius-Kühn-Archiv

Ulrich Darsow

Pre-breeding and breeding of potatoes for quantitative resistance to *Phytophthora infestans* on foliage and tubers and for different utilization - problems, solutions and results

Julius Kühn-Institut
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Bibliografische Information der Deutschen Nationalbibliothek

Die deutsche Nationalbibliothek verzeichnet diese Publikation in der Deutschen Nationalbibliografie: detaillierte bibliografische Daten sind im Internet über http://dnb.d-nb.de abrufbar.

ISSN 1868-9892 [Druckausgabe]

ISSN 2199-921X [Internet]

ISBN 978-3-95547-000-5

DOI 10.5073/jka.2014.441.000

Printed in Germany by Arno Brynda GmbH, Berlin

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1. Introduction and economical damage caused by late blight

1.1 Introduction

Since about 80 years two types of late blight resistance are known (see chapter 2.1.) The longer known type is of quantitative nature, largely effective against all pathotypes of *Phytophthora infestans* (Mont.) de Bary and durable in opposite to the race-specific hypersensitivity, which ran aground because of being effective only few years. However, exploiting of quantitative resistance in breeding is less attractive because of more complicated methods of assessment, low part of resistant progeny and only partial protection. Therefore breeding success using wild species as donors of resistance is slowly and takes long time. Many institutes and breeding enterprises worked on it temporarily, but not uncompromisingly and persistently enough. Only on very few places solid knowledge is accumulated as precondition for successful use. Durable late blight resistant potato could more contribute to nourishing of mankind and to conserve environment, sustainable to grow potatoes and to preserve human health.

The aim of pre-breeding for quantitative late blight resistance at Gross Luesewitz was to find a way for combining late blight resistance based on polygenes from wild species with other important traits in pre-breeding, which was started in early 1960ies. GDR planned self-sufficient solution in long-term work, complexly supported by applied public research and public cultivar breeding (Darsow 2000a, 2008). It was open, whether polygenic determined late blight resistance can be transferred from wild species to *S. tuberosum* genome and be preserved on effective level in combination with cultural traits or not. The encouraging answer is given in framework of pre-breeding at a near cultivar-level (Darsow 2008), not by cultivar breeding so far. And the answer is: yes, but difficult, with increased demand and costs. Our practical results contradict the common scientific meaning about biological possibilities and practicability of using polygenic resistance (Muskens & Allefs 2002, Allefs et al. 2005). In addition, an important argument for necessity of gene technique as allegedly sole promising solution is baseless due to here submitted results.

Therefore current results of a life-long pre-breeding based on quantitative late blight resistance on foliage and tubers are presented here. Intention of this script is to transmit methodical details necessary to go on successfully in very difficult using of quantitative late blight resistance. Furthermore the chances of this type of late blight resistance are shown. The script informs how successful pre-breeding for long-day and temperate climate has been conducted at Gross Luesewitz, Germany, since 1964 (chapter 4.2., 4.4., 5.3., 5.4., 6.). The current results of pre-breeding for resistance as the most environmental–friendly measure of plant protection are given in chapter 7 and 8. Reasons for globally insufficient contribution of late blight resistance (3.3.) up till now in cultivar-breeding are analysed (3.2.) in spite of long breeding history (3.1.). The current state of research is summarized (chapter 2.). Known methods to assess late blight resistance are reviewed (4.1.-4.4.). The very old problem of relation of foliage blight resistance to maturity was solved in our pre-breeding practice (2.5., 4.2.4.). Mainly chapter 5-8 are a changed repeat of a publication in German language (Darsow 2008). Recommendations for pre-breeding on EU-level and for cultivar breeding are given (9.). Social trends complicate the use of the hopeful quantitative late blight resistance type (10.3.).

The Institute of Breeding Research on Agricultural Crops Gross Luesewitz near Rostock is part of the Julius Kuehn-Institute, the Federal Research Centre for Cultivated Plants, which was named before 2008 Federal Centre for Breeding Research on Cultivated Plants (BAZ). Therefore all mentioned breeding clones, which are bred before 2008, are named BAZ-GL-number. This script is written after retirement of the author in 2007 dealing with late blight since 1969, with pre-breeding for blight resistance since 1972, which is continued here (Hammann & Thieme 2011).

Used abbreviations and some terms are explained at the end. An index supports looking for special context or terms.

1.2 Damage by *Phytophthora infestans*, costs of protection against it and possible effect of mainly quantitative host resistance to replace fungicide application

Since 1840ies dramatic losses in potato production caused by *Phytophthora infestans* (Mont.) de Bary are drastically reduced in most parts of the world. However losses and costs of protection are lesser decreased than expected (Oerke & Dehne 1997) and potato late blight will continue to cause food shortages and hunger in several parts of the world (Garelik 2002). Potato late blight epidemics in the Netherlands are analysed from 1950-1996 and showed missing progress in disease control (Zwankhuizen & Zadoks 2002). During 31 years (1952-1982) at Hoefchen, in South East from Trier, Germany, late blight incidence of 100% on potato happened without chemical protection in 16 years. Chemical control increased yield by 20% and starch content by 0.5% in average of 40 years at that location (Kolbe 1982/83).

Looking at the present-day situation, late blight continues to be the most important potato disease in the world (Innes 1995, Niederhauser 1999). Guenthner et al. (2001) estimated costs of potato protection against blight to the potato growers in USA of $507 per hectare potato per year, in which oomycide costs, yield decrease, storage losses, quality decrease and price adjustment are considered. However, losses because of apparently other tuber rots or mixed rots are not included, in which tuber blight was the primary and inducing step overgrown by mainly soft rot (Sicilia et al. 2002). For Germany costs of 470 € per hectare potato were estimated, in which 150 € represents the price of oomycides and its application, 250 € the yield decrease and 70 € the loss because of tuber blight (Darsow 2002a). Costs of late blight in potatoes in the Netherlands from control and not prevented loss are calculated with 16% of total farm gate price (Havercort et al. 2008, 2009). Up to 20% of total production costs are required for controlling late blight in Brazil (Mizubuti et al. 2002), and nearly 30% for chemical protection of susceptible cultivars in central Mexico (Rivera-Pena 2005). Pathogenic resistance to some protecting chemicals is an additional problem (Ziogas et al. 2006). The yearly crop losses due to *P. infestans* (Mont.) de Bary for Belarus were estimated up to 80% in years with sever blight (Anoshenko 1999). Six to 16 applications of oomycides to control oomycetes are used per vegetation in Europe (Schepers 2004a). Losses of nearly $3 billion were calculated for developing countries (Anonymous 1996). Some European countries decided about 15 years ago more to restrict chemical plant protection to reduce negative effects on environment and ground water (Spiertz et al. 1996, de Vries 1996, Schepers et al. 2000, Kessel et al. 2004, 2006, Cooke et al. 2011a). However, in Finland the sales of blight oomycides were increased almost fourfold compared to 1980ies (Hannukkala et al. 2003a). Compared with the late 1970s the chemical applications to control late blight in Europe were in 2000 about 40% higher (Flier et al. 2002); the intensity in most countries increased additionally up till now (Cooke et al. 2011a). In organic farming late blight is a limiting factor of economic potato production (van der Zaag 2010) and host resistance it's most important measure of protection (Finckh et al. 2006).

Quantitative late blight resistance is able to substitute for as much as 80 % of oomycide application against late blight (Bus et al. 1995, Clayton & Shattock 1995, Gastelo & Landeo 1999, Kirk et al. 1999, Ordoñez et al. 1999, Rodriguez & Garcia 1999, Gruenwald & Fry 2000, Cooke et al. 2001, Kirk et al. 2001, Nærstad 2001, Hansen et al. 2002b, Kapsa 2002a, Gans 2003, Kessel et al. 2003, 2006, Nielsen 2004, Wander et al. 2006) in integrated plant protection. According to the own expectation one third of oomycide effort should be saved (replaced) by more quantitative resistant new cultivars bred with pre-breeding clones of the ZL (ILK) Gross Luesewitz (Darsow 2002a), possessing mainly second-early to early maturity and sufficient quality.

2. Disease, resistance and pathogenicity

2.1. Qualitative and quantitative resistance to *P. infestans* (Mont.) de Bary

Potato, *Solanum tuberosum* ssp. *tuberosum* (*tbr*), is a tropical perennial plant, which is functionally annual concerning leaves and stems (Robinson 1976). The potato disease caused by *P. infestans* was first time described by Jose de Acosta 1571 from the Andean plateau near Bogota and Peru (Vowinckel 1926, Kolbe 1999). In the 1840's the potato late blight pathogen burst out of its native home in Mexico, and attacked the potato crops in North America (1843) and was distributed from there with seed potatoes to West Flanders in Europe (1844). The disease destroyed the potato crop as basic food with tragic consequences in 1845 and following years (Zadoks 2008). This disease gave a strong impetus to development of phytopathology and to potato breeding because potato became probably the first plant in which breeding for resistance was attempted (Salaman 1911, Hawkes 1994).

P. infestans belongs to the Oomycetes in the kingdom *Chromista* and was firstly detected by M.A. Libert in 1845 and finally named by de Bary (1861). The pathogen is heterothallic; A1 and A2 mating type occur in large parts of the world (Hohl & Iselin 1984, Fry 2007). *P. infestans* lives hemi-biotrophic and infects parts of the potato plant above and below the ground, known as late blight of foliage (fig. 1) and of tubers (fig. 2). The duality of potato late blight as disease of foliage, and in view of breeding relatively independent on tubers, complicates control measures including breeding for resistance. Lesions on leaves start as a water-soaked, poorly defined spot, which changes to brownish grey and are surrounded with white aerial mycelium mainly on the underside; the lesions expand and become dark brown, irregularly shaped roundish spots. Stalks and stems may be affected and turn brown (fig. 3). Colour, smell and sporangiophores with sporangia are used for identification. Under moist conditions a potato crop may be entirely destroyed within two weeks. Tuber infections first are detected as bluish marks showing through the skin, few days later affected tissue turns rusty brownish, the pathogen may spread in the whole tuber and frequently is followed by other pathogens as *Erwinia* sp. or *Fusarium* sp., which can overgrow *P. infestans*. Diverse descriptions of potato diseases are available for more details.

Host resistance is defined as the ability of the host to hinder a pathogen or disease causing agent (Robinson 1969). Hindering can occur in all stages of pathogenesis. On a compatible host sporangia or motile zoospores swim on the leaf surface in a water drop, encyst, and germinate. Germ tubes form an appressorium and then a penetration peg, which pierces the cuticle and penetrates an epidermal cell to form an infection vesicle. Branching hyphae expand from the site of penetration to neighbouring cells through the intercellular space; haustoria penetrate the potato cells. Intensive metabolic interaction leads to necrotization of host tissue after intensive development of sporangiophores with sporangia, the main form of pathogen dispersal, which release zoospores under cool and humid conditions. Three spore forms (sporangia, zoospores, oospores) play critical roles in the life and infection cycle of *P. infestans* and greatly impact the epidemiology of late blight (Judelson & Blanco 2005). The molecular processes linked to adhesion on plant surfaces, penetration and colonization are, in large part, poorly understood (Kamoun & Smart 2005).

Passive factors of resistance as repulsing structures on the surface of foliage or haulm (Bonde et al. 1940, Huettenbach 1951, Brown 1955, Umaerus 1963, Zarzycka et al. 1978, Singh & Birhman 1994, Singh & Bhattacharyya 1995, Lai et al. 2000), the growth habit or canopy structure and density (Mueller 1931, Johannes 1953, Wastie 1991, Harrison 1992, Singh & Bhattacharyya 1995), epicuticular wax content and stomatal conductance (Mahajan et al. 1999) or thickness of tuber periderm, its lenticels structure or the state of the cork cambium layer (Loehnis 1923, Bonde et al. 1940) seem mainly not sufficient examined. They are expected to be not impor-

tant in using hypersensitivity but contribute to quantitative resistance (Johannes 1953, Harrison 1992, Mahajan et al. 1999). Likewise, research on active and passive reduction of penetration of *P. infestans* into potato tissue seems to be insufficient up till now (Umaerus & Umaerus 1994). There are questionable results too as stem diameter and phloem thickness of stems as components of quantitative foliage resistance of CIP's PD-population (Evers et al. 2003/04) with low level and low differentiation under long-day conditions.

Active resistance is assumed to play the main part in late blight resistance (Mueller & Boerger 1941, Tomiyama 1982, Umaerus et al. 1983). This resistance is not to imagine as a fixed trait or a state, but as a functional character, a genetically controlled reaction potential (in intensity and rapidity) as answer on penetration of the pathogen (Mueller 1940, Mueller & Boerger 1941, Mueller 1950a, Clark 1978, Parlevliet 1979, Buddenhagen 1981). In general, resistance is a livelong, variable repeated process of response, probably with reduced intensity at the end of vegetation (Mueller 1931, Robinson 1976). Intensive defence happens in physiological competition to processes connected with yield and quality (Mitra & Bhatia 1982, van der Plank 1984, Kern et al. 1987).

Two types of true host resistance of potato to *P. infestans* are distinguished: hypersensitivity as qualitative type and horizontal resistance as quantitative type (Gaeumann 1946, van der Plank 1956, 1963). Some synonyms to it are written in table 1, additional terms are discussed by Erwin and Ribeiro (1996), Forbes and Landeo (2006).

Table 1 Characterization of late blight resistance types and its synonymous terms

Terms of resistance	qualitative resistance	quantitative resistance
	hypersensitivity	partial resistance
	vertical resistance	horizontal resistance
	R-gene resistance	relative resistance
	race-specific resistance	un specific resistance
	complete resistance	rate-reducing resistance
	differential resistance	uniform resistance
	↓	↓
Characteristics of resistance		
Source of resistance	wild potato species	wild and cultivated species
Effective against pathotypes (races)	only against some special	against all
Defence reaction	complete protection	reduced disease
Environmental influence	low	high
Estimation of incidence	yes/no sporulation	quantitatively, components
Calculation of resistance from	incidence (differentials too)	regression rAUDPC/maturity
Inheritance of resistance	often monogenic dominant	mainly polygenic
Years of assessment	one year (1-2 tests per race)	3 years, different methods
		several isolates of the
		highest complex race
Durability of resistance	short	long to very long
Durability of resistance	one mutation step	complex of mutations
Duration to breed a new variety	30-40 years	more than 50 years

Qualitative late blight resistance based on hypersensitivity is an active form of race-specific or pathotype-specific resistance. Penetration into host cell occurs of an incompatible (qualitative resistant) as well as a compatible pathotype (quantitative resistant with different levels up to highly susceptible). The initially invaded host cell produces callose-like material within a few hours. Penetrations occur on or near the anticlinal cell walls (Mueller 1931, Rubio-Covarrubias et al. 2006) or stomatal guard cells (Mueller 1931). Up to this stage susceptible and resistant tissues react similar. Different reaction causes from the recognition of the pathogen by the host; recognition activates a signal transduction chain leading to defence reaction (Umaerus & Umaerus 1994). Once the spongy parenchyma is reached in the foliage differential responses are apparently. The difference lies in the intensity of metabolic reaction in invaded and adjacent cells; high intensive reaction results in rapid local cell collapse and brownish colouring of invaded and surrounded cells called hypersensive reaction (Mueller 1940, 1953, Kitazawa & Tomiyama 1969, Tomiyama 1982, Cuypers & Hahlbrock 1988, Gees & Hohl 1988, Schmelzer et al. 1995, Kamoun et al. 1999). Lesions generally do not extend beyond a few cells, and *P. infestans* cannot produce sporangia. However, different reaction speed occurs in different potato tissues and different environmental conditions (Mueller 1950b, Harrison & Lowe 1995), but these effects are smaller than in quantitative resistance. A complication means co-operation of an additional gene, in case of R1 of a dominant suppressor (El-Kharbotly et al. 1996). Nevertheless, deviations from the clear yes/no-reaction of sporangia development are sometimes a problem in assessing of R-genes by means of well defined races or virulence with known differentials (Toxopeus 1958, Schick & Schick 1959, Denward 1967, Swiezynski et al. 1974, 1996, Mooi 1977, Schoeber 1990). Races or pathotypes are subdivided by assessing on differentials, which were selected from hybrids with wild potatoes (Schick & Lehmann 1936, Lehmann 1938b, Mueller 1949, Black et al. 1953, Mastenbroek 1953). Very sparse sporulation on leaves of hypersensitive hosts in stage of progressed maturation is possible (Mueller 1933) and on some R-gene bears more than on others (Harrison & Lowe 1995). Since vertical resistance is usually controlled by a single dominant gene (Mueller 1930, Lehmann 1941, Black 1952, Black et al. 1953, Mastenbrock, 1953), mutation in one locus for avirulence (Avr) of the pathogen changed it to virulence (avr) and results in a new race capable of infecting foliage and tubers of the cultivar resistant up to now (Schick 1932, O'Connor 1933, Wriedt 1955, Schick et al. 1954, Graham et al. 1961, Schick & Hopfe 1962, Turkensteen 1993). Progress in breeding for R-gene resistance therefore quickly followed development of new races (Mueller 1935).

The terms qualitative pathotype or race mean forms of the pathogen which can be differentiated by means of differential potato clones (the pathogen sporulates or does not sporulate) and characterized in its qualitative pathogenicity (Mueller 1935, Schick & Lehmann 1936, Black et al. 1953). Its reaction is determined by genes for qualitative pathogenicity with the alleles for avirulence/virulence (Avr, non-pathogen/avr, pathogen), complementary to the host genes of hypersensitivity (R-genes/r, resistant/susceptible). The R-gene in the plant triggers hypersensitivity, when it recognizes signal molecules (elicitors) coming from Avr (avirulence) of the pathogen. The plant does not react hypersensitively when the signals come from avr, a compatible and therefore pathogenic isolate. The host/pathogen reaction follows the gene-for-gene-hypothesis of Flor (1955, Spielman et al. 1989, 1990), but Umaerus and Umaerus (1994) hint to deviating results. A potato clone with R1rrr (tetraploid, simplex R1) is susceptible to pathotypes with avr1avr1, recessively virulent. Small letter in avr means the pathogen is not recognized by the host. Avirulence Avr is dominant to recessive virulence avr expressed in the pathogen Avravr (Al-Kherb et al. 1995). Isolates with additional recessive avr as avr1.3, avr1.2.3.4.7, avr1.3.10 are pathogen to R1rrr too. However, all pathotypes without avr1 are avirulent to R1rrr. A clone with the combination of R1-R10 is resistant to 1023 different races with avr-genes 0-10 single and its possible combinations up to nine numbers, only the pathotype possessing avr1.2.3.4.5.6.7.8.9.10 or more avr-genes can cause late blight with sporangia production on it. However, hypersensitivity can be controlled by more genes than only R-genes, i.e. additionally

by modifiers or suppressors (El-Kharbotly et al. 1996, Ordonez et al. 1997). Qualitative resistance acts against all spores of incompatible pathotypes and reduces in this way drastically the effective inoculum from outside (allo-infections, Robinson 1979). The higher the number of combined R-genes in a clone the higher is the part of defended inoculum, but the higher is the selection pressure for new, compatible pathotypes.

Qualitative resistance is dominantly inherited and gives in crosses of simplex resistant x susceptible parents about 50% resistant individuals in the progeny. Resistance breeding based on R-genes was initially highly successfully due to its simple Mendelian inheritance. Protection of potato against late blight was assumed to be possible alone by breeding (Mueller 1928, 1930, Reddick & Mills 1939). Few years later resistant cultivars and breeding clones were rendered susceptible, new races or qualitative different pathotypes of *P. infestans* caused incidence (Schick 1932, Salaman 1949a, van der Plank 1984). A set of differential hosts was developed (Schick & Lehmann 1936, Mueller 1949, Black et al. 1953). During the following 30-40 years one had been learned that hypersensitive type of resistance acts too short time till adaptation of pathogen population by mutation and other mechanisms to new genes of virulence (Rudorf & Schaper 1951, Schick et al. 1958a, Simko et al. 2007). Still Mueller and Black (1952) regarded the rapid accumulation of all available major genes for hypersensitivity in varieties and exclusion of intermediate types of resisters as essential weapon for combating blight. The methodical development of DNA-based markers promoted genetic knowledge of qualitative resistance and selection for it. Twenty R-genes, conferring qualitative potato foliage blight resistance, have been placed on a molecular map of potato up to 2007 (Simko et al. 2007).

All known genes of this type of resistance of plants encode only five classes of resistance proteins (Simko et al. 2007). It has been estimated that the potato genome contains at least 100-200 genes of this class (Gebhardt & Valkonen 2001). The similarity in the location of R-genes to *Phytophthora* species in potato, tomato and pepper suggests possible evolutionary conservation of resistance genes. The tomato genome-sequencing will provide additional valuable information for cloning of more qualitative potato resistance genes. Nine R-genes are clustered in the late-blight resistance hot spot on the distal part of potato chromosome XI, some on chromosomes IV, V, VI, VII, VIII, IX, or X (Li et al. 1998, Bisognin et al. 2005, Huang 2005, Park et al. 2005b, Smilde et al. 2005, Bradshaw et al. 2006a, Sliwka et al. 2006a, Simko et al. 2007, Zarka et al. 2009, Trognitz et al. 2010). As opposed to other R-genes *Rpi-blb1*, *Rpi-blb2*, *Rpi-blb3* and *Rpi-abpt* from *S. bulbocastanum* are described as broad-spectrum resistance genes, which gave new hope for resistance breeding (Naess et al. 2000, Kuhl et al. 2001, van der Vossen et al. 2005, Song et al. 2003, Park et al. 2005a). New R-genes to which present population is not adapted, of course make for a short time a broad-spectrum effect. Claimed broad-spectrum resistance is on the one hand very unexpected and hard to belief concerning late blight, on the other hand by regulations connected with patents not to reconsider from outside. Nobody could exclude an only short duration of this resistance in future practical growing. There are some circumstances which may cause results too well at the moment, for instance testing in a too early stage, testing in very small plot, use of isolates not most fit (Gu et al. 1992) or with to low inoculum density, use of selected components of pathogenicity (Andrivon 1998). First results are known for resistance to reduced race spectrum of the new R-genes from *S. bulbocastanum* as expected by us (Lozoya-Saldaña et al. 2005, Oosumi et al. 2009, Halterman et al. 2010).

A similar situation was probably given by first hint on non-host resistance of *S. nigrum* (Colon et al. 1993). Own examination a few weeks later on plants collected in our region resulted in only about 40% resistant plants after inoculation with a highly virulent and aggressive isolate used for selection of our pre-breeding material. So the use of its non-host resistance was finished very quickly for us. Moreover, Vowinckel (1926) found *S. nigrum* to be a host of *P. infestans*.

By contrast, quantitative resistance (see table 1) acts in compatible host/pathogen relation usually connected with limited colonizing of the host and is caused by a complex of several ap-

parently independent factors (components) and expected to be determined by polygenes in the plant (Stevenson et al. 1937, Black 1970, Schick & Hopfe 1962, Parlevliet 1993). However, in some cases quantitative resistance may express morphological and cytological symptoms similarly to hypersensitivity (Umaerus & Umaerus 1994). Lapwood (1971) distinguished between directly killed leaves and indirectly killed ones, which were early damaged on the vascular system of a leaflet causing leaflet yellowing and dying. Quantitative resistance may include inhibition of zoospore germination, of appressorium formation, penetration, tissue invasion, or/and sporulation (Thurston 1971). It seems that the first period up to penetration is not enough investigated. More callose formation on the point of entry and smaller haustoria, encased by wall-like material can occur in resistant material (Hohl 1991). However, often differences are only observed in the extension of hyphal growth, its branching and sporulation (Berggren et al. 1988). Wilson and Coffey (1980) emphasized reduced penetration frequency and localising of the pathogen within leaf epidermis cells as most important components of quantitative resistance. Abortive penetrations occur in different frequency, the reason could be physical surface properties or the composition of the walls (Gees & Hohl 1988). Corresponding methodical aspects are considered in chapter 4. An unknown number of genes and possibly several mechanisms contribute mainly in small extent to the finally expressed phenotype. Several directional mutations would be required in the pathogens quantitative pathogenicity to reduce host defence quantitatively and therefore this type is durable (Robinson 1973, Parlevliet 1993, 2002, Turkensteen 1993, Umaerus & Umaerus 1994). Durable disease resistance in plants has been defined as resistance that remains effective while a cultivar possessing it is widely cultivated (Johnson 1981). Plant protection by quantitative resistance is only partial and is highly influenced by environmental factors and is changing with plant age (see chapter 2.4.). Therefore, often supporting by application of oomycides - frequently in reduced dosage or/and at longer intervals - is necessary (Bus et al. 1995, Clayton & Shattock 1995, Gastelo & Landeo 1999, Kirk et al. 1999, 2001, Ordoñez et al. 1999, Rodriguez & Garcia 1999, Gruenwald & Fry 2000, Cooke et al. 2001, Nærstad 2001, Hansen et al. 2002b, Kapsa 2002a, Gans 2003, Kessel et al. 2003, 2006, Nielsen 2004, Wander et al. 2006). Forbes et al. (2005) have been able to demonstrate that quantitative resistance in cultivars from the Netherlands, Scotland, Peru, Colombia and Mexico was partly stable across locations representing a wide range of latitudes and altitudes.

Components of quantitative resistance may be effective as resistance to entrance described as infection efficiency, resistance to spread of the pathogen in potato tissue measured as lesion growth rate, prolonged generation interval (often called incubation period or latent period) as duration between inoculation and begin of sporangia production, and reduced sporulation capacity as measure of resistance to sporulation (Thurston 1971, Russel 1978, Colon 1994). The components of resistance seems more (van der Zaag 1959) or less independent from each other (Lapwood 1961a, Main & Gallegly 1964). The polygenes operate at different stages of the disease progress (Wastie 1991). To combine different components, its separate assessment is advantageously (Hodgson 1962). The assessment of quantitative resistance requires much higher effort and experience of persons responsible for testing, and gives results with statistical probability for the true resistance. Applied methods are analysed in chapter 4.

Potato plant parts differ in its level of resistance to *P. infestans* within and between cultivars and breeding clones; in average they rank from most to least invaded in the following order: flowers, lower leaflets, upper leaflets, tubers and stems (Porter et al. 2004). Already Mueller (1931) pointed out that resistance of potato is highly intensive in juvenile stage of potato plant and reduced in maturing foliage as well as in tuber pith – both as equilibrium resulted from coevolution of host and pathogen.

Wild and cultivated species of *Solanum* are sources of quantitative resistance. In cross of polygenic resistant wild clone x susceptible cultivar the main part of progeny is highly resistant, but in following backcrosses to the cultivated potato the outcome of resistant part drops down with the distance to the wild species as source of resistance up to below 10%. As a quantita-

tive trait, highly influenced by environment and variable pathogen, it is much more difficult for breeders to work with it compared to dominant R-genes. Calculation of quantitative foliage blight resistance by regression of incidence level to maturity (see table 1) is necessary for assessment in long day conditions and will be discussed later (see chapter 2.4, 4.2.4). Additional breeding problems come from unintentional taking over of many genes with negative impact in most traits by crossing with wild species as source of resistance. Moreover, reasons of complication are the tetraploid level of potato, different components of resistance, necessity to combine the resistance with nearly 70 other traits and the fact that heterozygote allele constitution supports best performance of potato. Replacing the "wild" alleles of hybrids for most traits by desired ones without loss of most alleles governing quantitative blight resistance is the most complicated tasks in potato pre-breeding. Nevertheless, successful conventional breeding based on polygenic late blight resistance is possible according to results of ZL Gross Luesewitz shown in chapters 5.2.-8.

In table 1 given duration necessary to breed a new resistant variety is calculated for conventional breeding from identifying of suitable source of resistance among wild potato species followed by introduction of genes for resistance into the cultivated potato genome by crossing or fusion, which is followed by several generations of backcrossing alternated by inter-crossing, if quantitative and durable resistance is used (chapter 6).

If only a part of the used inoculum (or naturally occurred isolates) is compatible to the tested potato clone(s) the frequently existing situation of "field resistance" is given. This term is used without guarantee for or knowledge of the acting type of resistance and is therefore not identical to quantitative resistance as we use it. Such field resistance was and is frequently the base of potato breeder's hope in past and at present, with disenchantment after few years.

The effects of oomycides and of quantitative host resistance complement each other; reduced infection efficiency, reduced rates of lesion expansion and sporulation have been demonstrated with both (van der Plank 1968, Fry 1975).

2.2. Epidemiological aspects for assessment of potato late blight resistance

The aerial phase of late blight occurs on or in plant leaves, stems, pedicels, flowers and berries as spores or mycelium on potato and some weedy hosts. Spores produced on foliage are washed into or on the soil to infect tubers or plant debris and start living of the pathogen in soil. Zoospores actively move in the soil and live short time. Sporangia production on tubers in the soil is known mainly through lenticels of tubers (Parmentier 1967, Fedotova et al. 1975, Cupsa et al. 1984, Zellner 2000). In warm regions foliage and tuber infections occur around the year. Dryness is considered one of the greatest hazards to survival of mycelium, sporangia and zoospores (Fernández-Pavía et al. 2004). Mycelium may delimited survive saprophytically on plant debris. In case of temperate climate overwintering is the bottleneck in the live cycle of the pathogen and that is mainly connected with alternation from pathogenesis on foliage to tubers with wholly quite different conditions. Mycelium passes the winter in volunteer potato tubers in the ground or in seed potato tubers in storage. Alternatively the pathogen may survive several years as oospore on host material or in soil. On a leaf an asexual pathogen unit lives about 1-3 weeks, in a stem up to nearly eight weeks, and in a tuber up to about 11 month in storage. During optimal storage conditions partly no visible symptoms are developed on latent infected seed tubers, which are in temperate climate usually the major source of primary infections of foliage (Adler et al. 1999, Zellner et al. 2011). This situation would be aggravated by increased tuber blight resistance. According to van der Zaag (1956) infected tubers of middle tuber blight-resistant varieties produce only about 10% infected stems as primary source of early field infections compared with susceptible ones (Bintje). Therefore better resistance of tubers is the key for more effective use of higher foliage resistance (van der Zaag 1956). In absence of tuber resistance application of copper on tubers before planting can reduce early stem

blight infections by 37%; in conventional production early chemical protection of the haulm can reduce early stem blight (Zellner et al. 2011).

Additionally, oospores in the soil can survive the winter conditions in Canada (Medina & Platt 1999) and Sweden. Temperatures of -80°C longer than six days followed germination (Anonymous 2000/01). Oospores can infect underground stems and tubers in soil over several years after its germination via sporangium (Lapwood 1971, Stroemberg et al. 1999, Fernández-Pavía et al. 2004). In other climates oospores on the haulm occur preferred towards the final stage of the epidemic (Cohen et al. 2000, Stroemberg et al. 2001). In Mexico slow disease progress and long epidemic duration promoted abundant formation of oospores on leaflets, which was supported by chemical protection, environmental conditions or/and foliage resistance (Romero-Montes et al. 2008). Oospore germination in temperate climate is low, however, in warmer regions higher (Gupta et al. 1999, Anonymous 2000/01). After germination sporangia are developed.

From tubers to foliage *P. infestans* passes not only by growing into the sprout (van der Zaag 1956, Adler et al. 1999) and within the stem (Peterson 1947, Ratanen et al. 2001). Primary leaf and stem infections may be caused by tuber-borne spores on wet soil (Haenni 1949, Parmentier 1967, Rotem & Shabbath 1972, Boyd 1980, Sato 1980). Beyond it, daughter tubers may be infected directly from sporulating mother tubers (Zellner 2005). Only saturation near 20% of water holding capacity in the soil is optimal for *P. infestans* (Zan 1962). On cultivar Cara in Ireland local adaptation of the pathogen population was obtained which resulted in higher aggressiveness on tubers (Dowley et al. 1991). Quantitative pathogenicity (aggressiveness) of *P. infestans* isolates can differ for foliage and tubers (Cadish & Cohen 1992, Flier 2001, Flier et al. 2003a). Higher aggressiveness of "new population" on tubers compared to old isolates was found by Flier et al. (1998). However, only isolates which combine a balanced pathogenicity on foliage and tubers with overall fitness (as oospore too) are best log-term adapted. Increased aggressiveness resulted in competitive advantage in a season with increased danger to kill the host and reduced chance to survive the crop-free season or low frequency on foliage and very high frequency of killing tubers before emergency after planting (Thompson & Cooke 2005).

The most important climatic factors are wetting duration and temperature; both mainly restrict spore production and infection (Rotem et al. 1971, Harrison 1992). Zoospores are released from sporangia, the other form of vegetative spores, after chilling an aqueous sporangia suspension. This indirect germination increases the available inoculum units about tenfold nearly optimal at about 11°C, but zoospores may swim only very short time before they encyst, adhere to the host surface, germinate and penetrate into host tissue. At 24°C zoospores are up to 19 minutes motile (Melhus 1915). Sporangia and zoospores germinate only in the presence of free water. Zoospores quickly loose their infectivity in the absence of free water. Within the inoculum drop they have to move to a suitable point of penetration. Therefore, a conclusion for large scale-test procedure in breeding is to subdivide the suspension in several equivalent parts that one part after staying two hours in the refrigerate at or below 11°C is used not longer than 15 minutes; then the next part of zoospore suspension is taken from cool conditions.

Infection at 21°C requires at least 2.5 hours contact of the inoculum drop; after 4.5 hours duration of inoculum droplets on leaves of a susceptible cultivar 50% caused infection and later on sporulating lesions (Crosier 1934, Harrison 1992). A longer duration and higher dosage are necessary for highly resistant breeding material (Umaerus 1969b). Wetting duration in inoculation has to be long enough to ensure a desired disease level, but its limitation, together with the lower temperature prevents rotting from other pathogens, first line in whole tuber test and single-leaf test. Too long covering of seedlings after inoculation increases the effect of low light intensity. While infection of foliage occurs mainly by zoospores, direct germination of sporangia may play a role in infection of wounded tubers (Schoeber & Ullrich 1985).

For field assessment good knowledge of environmental conditions is necessary to induce the disease and to regulate its course. Sporangia are formed between 3°C and 26°C, most rapid and abundant at 21°C (Crosier 1934), and near the temperature optimum at humidity slightly below saturation too (Harrison 1992). On the leaf surface sporangia survive adverse conditions better than assumed commonly, more probably on shaded lower leaves (Waggoner & Shaw 1951) and they are longer infectious there (Tverskoy et al. 1981b). In stem lesions mycelium survives temperature of 43°C for an hour, of 32°C for 40 days (Ullrich 1957, Harrisson 1992). Unfavourable conditions stop the spread of foliage late blight, but do usually not eliminate the pathogen mycelium in stems or tubers between -3°C and 40°C (Kirk 2003). Under unfavourable conditions Kapsa (2001) found stem isolates much more aggressive compared to leaf isolates. While the old population caused infections at 8-23°C, the new population in the Netherlands infected at 3-27°C (Flier et al. 2001).

Rain, drizzle, fog, mist, and dew result in wet foliage and increase humidity within and above the haulm. Humidity, together with wind and irradiation, affects the rate of drying of wet plant surfaces. But air next to the stomata of a turgid potato leaf is saturated even when the leaf surface is dry, and air immediately to the cuticle between stomata is close to saturation. Transpired water vapour is removed from the air close to the leaf more efficiently with decreased ambient humidity and increased air speed, influenced by leaf geometry (Harrison 1992). High relative humidity is obtained round the clock first of all within the crop and is preserved there longest time with frequently the highest values near the soil and highest range on the top (Johannes 1953). Sporangia remain viable for several hours after deposition on leaf surface, even when the ambient air is dry (Wallin 1953), but loss their viability irreversibly in air at or below 95% RH within a few minutes (Warren & Colhoun 1975). A minimum period of three hours of free moisture on leaves is necessary for infection with high inoculum density and optimal temperature (Ullrich 1957, Rotem et al. 1978); at 10°C six hours wet duration were at least required to infect a susceptible cultivar (Rotem et al. 1971). Inoculum drop duration of half an hour at 95-100% RH resulted in 1% leaf spots but 28% spread from axil inoculations as later stem infections (van der Zaag 1956). Under marginal conditions overhead sprinkling encourages blight, and morning irrigation had the greatest effect (Rotem et al. 1971). Prolonging of wet duration by irrigation has to start before dew begins to dry up and in the evening not too long before dew is effective. Successful field inoculation requires probably about 10 hours remaining of inoculum drops on the leave; new infection cycle or wave from a few days old lesions will take nearly 9 hours wet duration for sporangia production and additional 5-10 hours for spread, zoospore release, encystment, germination and infection (Ullrich 1958).

Abundant sporangia are formed at low air speeds when the ambient humidity is 90-100%, but not at 85-95% RH and higher air speeds (Harrison 1992). Free water is not required for sporangia formation (Harrison & Lowe, 1989), but about 9 hours very high air humidity enable intensive sporangia production (Stephan 1982). At low wind speeds dew forms at a lower ambient RH supported by transpired water vapour around the leaves (Collins & Taylor 1961), but darkness slows down evaporation. Dew covers both sides of the leaves (Ullrich 1957). Ullrich (1958) obtained dew mostly intensive on the surface of the potato crop; longer wet duration deeper in the crop was caused by at least 0.25 mm rain.

Small droplets with spores may caused by dew and are saved longer in leaf axils on the stem from drying than on leaves and causes therefore mainly stem infections (van der Zaag 1956). Cultivar-specific differences in frequency of infections in leaf axils and on stem tops have been mentioned (Lapwood 1961a, b, Ullrich 1968). Continuous variation of temperature and humidity in the field complicated estimation of its effect in assessment of resistance. The field design for assessment of foliage blight resistance has to take into account the main wind direction (Schroedter 1954); preferred spore spread may be supported in parallel to the potato hills. A ridge spacing of 62.5 cm instead of 75 cm may favour the microclimatic conditions for the pathogen (Schoeber 1976); the same due to smaller path between plots.

The diurnal periodicity of spore production of *P. infestans* (De Weille 1962, Harrison 1992) has to be considered in preparing the inoculum and inoculation. Sporulation is not induced by darkness, but is inhibited by high light intensity during the day; spores are mainly formed at the night (Harrison 1992). Humidity change is the main cause of sporangial release. Sporangia dispersal in the field starts in the morning and has a maximum before midday (Hirst 1953, Lapwood 1971). In the evening flying sporangia are probably more infective than such from the morning (Bashi et al. 1982). Most absorbed radiation heats the potato tissue and high-intensive radiation kills the spores (De Weille 1963, Mizubuti et al. 2000).

Main factor of sporangia dissemination is the wind. Distances of 90 m to 225 km are proved (Schroedter 1954). Low wind speed disseminates propagules on small distances. Near-distance distribution occurs mainly with rain drops or splashes. In the potato crop sporangia land about 10-30 times more frequently on the upper leave side than on the underside (Umaerus 1963). If they are blown in from other field parts most sporangia are deposed on the upper leaves, otherwise more on that of the middle and under plant part. However, infections are lesser effective on the upperside of the leaves than on the adaxial surface, a relation of 3-8 times frequenter infection was found on the underside (Bjoerling 1958). A 2.8 times higher infection rate stated Vowinckel (1926) on the underside. Infection occurs mainly in the stoma complex (Gees & Hohl 1988).

A number of 1480-1780 sporangia/cm^2 produced on leaves counted Carnegie and Colhoun (1980). Up to 139,531 sporangia were produced on a single leaflet of Bintje in the laboratory and 75,793 sporangia on a whole plant in greenhouse (Harrison & Lowe 1989). Up to 141,000 sporangia per lesion were counted from a field grown leaf by Bashi et al. (1982), up to 33,417,000 sporangia are produced by 1300 potato plants per day and up to 836 sporangia per m^3 air above a potato field. Iglesias et al. (2010) registered up to 145 sporangia per day and m^3 1.5 m above a potato plot. Maximal oospore count in the field was 200 per leaflet, but ranged from 2000 to 12 000 in the laboratory (Cohen et al. 2000). Up to 1091 oospores per cm^2 found Flier (2001) in laboratory conditions on *S. demissum*. Moderate oospore infestation of soil in the Toluca valley (20-39 oospores per g soil) resulted in higher number of stem lesions and higher initial disease severity (Fernández-Pavía et al. 2004). On cultivar Alpha in Calimaya, Mexico, in the field 4% *P. infestans* infected tubers were found and in it 10-15 oospores per tuber were observed (Fernández-Pavía et al. 2002). According to Suprun (1988) 8.5 x 10^{12} sporangia per day may be produced from a crop of one hectare potato. Under ideal conditions the *P. infestans* population could increase by a factor of 300,000 every four days (Fry 2007). On a cut surface of a tuber 100,000 sporangia may be formed (van der Zaag 1956). More than 2100 sporangia per ml were counted on soil surface after heavy rain on a potato field in September by Lacey (1962). At least five generations of *P. infestans* are necessary in the field under European conditions to infect potato plants of a large field completely from a few primary foci (Mueller & Haigh 1953).

Tuber infections occur in the soil before harvest (Stephan 1970, Nærstad et al. 2007) and during harvest and storage (Dowley & O'Sullivan 1991) in temperate climate. Before harvest tubers are infected after at least 5 mm of continuous rain and are more frequently blighted after one or two adjacent days with 13 mm of rain, if foliage is attacked (Lacey 1962, Hirst et al. 1965, Lapwood 1977). In the 1960ies was concluded that "the cover, lethal range, persistence and toxicity of fungicides (oomycides) now used against blight are such that the disease can not be contained when 1% of foliage has been infected" (Hirst et al. 1965). Now some oomycides are more effective (Stein & Kirk 2002), but a very low foliage blight level (0.1%) may be followed by a wide range of tuber blight due to prolonged period of sporangia production and increased probability of rain and dew to wash down the spores (Murphy 1927, Grainger 1957, Cox & Large 1960, Fehrmann 1963, Hirst et al. 1965, Lacey 1965, Lapwood 1971, 1977, Pietkiewicz 1978b). Karaseyeva (1979) calculated an increase of tuber blight by 0.18-0.25% per day of living and sporulating foliage from the end of flowering. Thus, the tubers of foliage blight resistant cultivars are at higher risk from infection, because sporulation on its foliage drags on longer.

The growth habit of cultivars influences if the spores mainly are washed down on the stem or mainly drop down from leave tips (Lapwood 1966, Lacey 1967b). In the first case lesser precipitation amount may be more effectively (Lapwood 1964, 1977, Bain et al. 1997), in the last the soil filters more spores and the transport way is much longer (Lapwood 1977). Moreover, sporulation on stem occurs quicker after dry periods than on leaves and is more effective for tuber infections (Lacey 1967b, Bain et al. 1997). That is strengthened by declining of sporangia number produced on leaves in disease progress, and simultaneously in contrast, by increased spore production on stems (Lammers et al. 1998). About six mm rain made the soil surface infective by washing down sporangia, 19 mm made it infective to 15 cm deep (Lacey 1965). The degree of tuber infections additional depends upon soil conditions including soil type (Zan 1962) and soil moisture (Lapwood 1965, Lacey 1967b), ridge form, the thoroughness of the earthing-up, distribution of tubers in the ridge (Lacey 1966), rigidity of the haulm (stems, Lacey 1966), frequency of precipitation (dew too) in presence of foliage blight (Cox & Large 1960), occurrence of chaps in soil (Zan 1962), soil temperature (Sato 1979), the time of lifting in relation to the blight attack on the haulm (Murphy 1927, Mueller 1957, Lacey 1965, Bochow et al. 1979), the used fungicides on haulm and method of vine killing (Bain & Moeller 1999, Nærstad 2002), the tuber susceptibility of the variety to *P. infestans* and to mechanical damage, the weather conditions at the time of lifting, the used technology of harvest, ventilation for surface-active drying of tubers before storage, storage technology and conditions. The infectivity of soils by sporangia can persist for 15-45 days (Andrivon 1994) or for two month (Evenhuis et al. 2006). As mentioned at the beginning of chapter 2.2, zoospores actively move in the soil and may infect daughter tubers from neighbouring plants (Jones et al. 1912, Murphy 1927, Zellner 2000) or from infected to healthy tubers of the same plant (Lacey 1962, 1967b, Cupsa et al. 1984). Viable sporangia have been detected on freshly harvested tubers (Murphy 1927, Lacey 1962). Tuber stolons can be infected by *P. infestans*, which is an additional way of entrance. Micro organisms in soil may markedly reduce pathogenic potential of *P. infestans* in soil for tubers in Toluca valley or in determined other conditions (Rivera-Pena 1990b, Adrivon 1994, Garzon & Forbes 1999, Fernández-Pavía et al. 2004).

The regional host range plays a role in population dynamics of *P. infestans* besides trade (Cooke et al. 2005). For instance, isolates from hairy nightshade (*S. physalifolium*) were found to be more aggressive than from potato (Groenberg & Andersson 2011).

40 late blight epidemics in the Netherlands between 1950 and 1996 could correctly be explained from blight status of the previous year and meteorological variables. Five out of six deviating years with unexpected high blight incidence occurred in the period after 1978, notwithstanding progress in disease forecast and control and increased fungicide application (Zwankhuizen & Zadoks 2002). Oospore development is one possible causal factor. First findings of late blight in the field occur one month earlier now than 20 years ago in Finland (Cooke et al. 2011a). Changing of climate and changing of agriculture are to consider besides oospore production to influence the development of pathogenic efficiency.

In a part of Asian countries potatoes are grown in sub-tropical climate with high temperatures, short days, dew and a range of rain. The late blight populations there change slowly and host resistance with R-genes remained effectively for decades (Singh 1999a). Highland tropics include tropical Andes, Central America, western equatorial and sub-Saharan Africa and parts of Asia with partly year-round potato cultivation mainly on small fields. Low night temperatures cause slower disease progress than in temperate climate (Lapwood 1971). Measures that delay initiation of the disease are here ineffective; therefore resistance plays here a more important role in plant protection and there exists an urgent demand for it (Lapwood 1971, Forbes 1999).

2.3. Stability of quantitative late blight resistance of potato

Van der Plank (1963) postulated that aggressiveness (quantitative pathogenicity) and virulence (qualitative pathogenicity) are strongly negative correlated, known as stabilized selection, which should make pathotypes most abundant, which possess the minimal necessary virulence gene combination and are at the same time the fittest. In this way unnecessary virulence gene combinations should kept scarcely. However, in populations of agro-ecosystems surplus of virulence gene combinations are commonly in populations from potato fields and allotment gardens (Frandsen 1956, Malcolmson 1969b, Shattock et al. 1977, Pietkiewicz 1978a, Parlevliet 1981, Tooley et al. 1986, Schoeber-Butin 2001, Cooke et al. 2011a, b). Already Mastenbroek (1964) found: "The relative aggressiveness of the races seems to be independent from their race character. Moreover, it does not seem to be stable for one particular race". That is confirmed manifold and complicated by the fact that the components of pathogenicity as the components of resistance vary partly independently from each other (Flier & Turkensteen 1999, Carlisle et al. 2002). Today pathologists can easier characterize isolates to other criteria than qualitative and quantitative pathogenicity, however these are of highest interest for resistance breeding.

Pathogens commonly adapt themselves to resistant varieties (Yarwood 1962). As an airborne and splash-borne, hemibiotroph pathogen with a very high propagation potential (1: 300 000 every 4 days under ideal conditions for the pathogen according to Fry 2007), *P. infestans* belongs to the pathogens with the highest potential for adaptation (McDonald & Linde 2002). The resulting danger for the potato crop is strengthened by vegetative multiplication of the host, enabling the permanent presence of compatible pathotypes on diverse potato clones without interruption during vegetation and at storage, or in soil as oospores over years and on volunteer plants or some weeds. In addition, a potato crop consists of one or few cultivars with genetically identical plants each, which causes a very high selection pressure on the pathogen population in case of resistant host. Monoculture enables quick spread of a new and competitive pathotype on it by auto-infections (Robinson 1973). Compared with the wild ecosystem the crop ecosystem requires a higher level of resistance because of much higher plant number per area. Higher growth rate and nutrition cause other micro climate and cell content. However, usually new specialised high yielding varieties possess the lowest quantitative resistance (Robinson 1976). On large potato fields quantitative resistance is more essentially than in agricultural structure with diverse small fields (Robinson 1976, Darsow 1983b, Parlevliet 1997, Zadoks 1993). Adaptation of the pathogen is a question of duration and acreage of growing a cultivar too (see 2.9.). However, a sudden break-down as R-gene resistance has never been observed and is not to be expected. The key to understanding durability of resistance is the population genetics of the pathogen, its reproductive system and variability (Zadoks 2002).

Durability of resistance is the first concern in late blight resistance breeding (Umaerus & Umaerus 1994). Durable resistance is defined by Johnson (1981) "as a resistance that remains effective while being extensively used in agriculture for a long period in an environment conductive to the disease." Adaptability of the population of *P. infestans* to quantitative resistance by stepwise increasing the quantitative pathogenicity is very difficult to examine and is excluded per definition by van der Plank (1963) and Robinson (1973). However, confronting results (Parlevliet 1976, 1981, 1983a, Parlevliet & Zadoks 1977, Russel 1978, Lebreton et al. 1999) suggest assuming low probability of adaptation. "In evolutionary sense no resistance lasts forever" (Parlevliet 2002). The speed of potential adaptation is important and the understanding of underlying mechanism to calculate the chance for success in breeding. That is work for future. Some researchers did not find such adaptation (Paxman 1963, van der Plank 1971, James & Fry 1983, Montarry et al. 2004); in contrast, other established small, significant isolate-cultivar interaction (Jeffrey et al. 1962, Riley 1973, Caten 1974, Darsow & Meinl 1981b, Jellis 1981, Latin et al. 1981). Very slow adaptation was expected by Black (1957) and Fry and Spielman (1991). Cox and Large

(1960) quote Niederhauser concerning the value of quantitative resistance in wild species: "Furthermore, the partial resistance that we have observed in *S. demissum* and other species has apparently been stable for many hundreds of years and has enabled these species to survive." However, in agro-ecosystem the selection pressure is manifold higher and is last decades additionally increased by oospore production (Andersson et al. 1998).

Stability or durability of quantitative resistance over long time includes interactions with environmental conditions (cultivar/year, cultivar/location) and varying pathogen population. The interpretation of stability often has a too high range of free discretion, for instance in an international study conducted in eight countries over two years and eight or 14 cultivars, respectively (Forbes & Tolstrup 1999). The trail design was only similarly - direct inoculation, inoculation of spreader rows or natural infection were applied - and therefore insufficiently comparable. Cultivar Stirling was very resistant with exception on three of eight localities; cv. Monserrate was resistant at seven and rather susceptible at one location. The cultivars Dutch Robijn, Pimpernel and Alpha varied from intermediate to susceptible. General experience is given that "cultivars with quantitative resistance have a large year to year variation, and there are indications of resistance efficiency loss in some cultivars. The experimental data so far indicates that horizontal resistance is relatively stable, irrespective of environment. Tropically resistant materials were found to be resistant in the temperate zone, and vice versa. The cases of instability that have been found till now seem to be isolated events." Relative constancy of resistance ratings of cultivars over time is described too (van der Plank 1971, Parker et al. 1992, Colon et al. 1995a, Inglish et al. 1996, Gruenwald et al. 2002, Landeo 2002, Forbes et al. 2005). Durability of resistance contributes to sustainable agriculture (Stuthman 2002).

A problem in clone-breeding (pedigree-breeding) of potato is erosion of genes mainly for quantitative resistance, which is strengthened by changing of the farming system, by changing of environmental conditions, by breeding for vertical resistance and by chemical plant protection (Robinson 1973, 1979). Combining of vertical and horizontal resistance makes sense, if horizontal resistance can be reinforced with a spatial and sequential pattern of different vertical resistant clones (Robinson 1973). Demand for increased host resistance usually resulted globally from changing agriculture development (monoculture) and distribution of pathogens and pests by trade; their negative effect is in reality higher than the progress in breeding for resistance (Harlan 1976). Remaining of endemic balance in agro-ecosystem reached by resistance breeding requires continuation of that breeding (Harlan 1976).

2.4. Variation of quantitative resistance by environment, ontogenic potato stage, other pathogens and micro flora on plant surface

Late blight disease is the result of a complex interplay of potato clone, compatible *P. infestans* pathotypes, environmental conditions and additional micro flora on potato plant and tuber surface and in its tissue. There is a differential reaction of host and pathogen to the environment (Yarwood 1962), which causes sometimes unexpected results, despite standardization and careful following the test protocol. The environmental effect on *P. infestans* is most critical during development of germ tube and penetration of the pathogen with free moisture as dominant factor. Environmental and ontogenic factors influence the reaction of the host (disposition) by current conditions and at the same time by after-effects of preceded environmental conditions (predisposition) as an intricate interplay of structural genes with regulatory loci (Tepper & Anderson 1984, Willmitzer 1987). Predisposition is interpreted as exogenic and/or ontogenic modification of the genetically determined resistance behaviour (Braun & Riehm 1957, Yarwood 1959). Research on influencing factors prior inoculation and during assessment of resistance is mainly described in the elder literature and partly repeated last 15 years. Several factors act at the same time with complex interactions on 1. the potato with partly cultivar-specific reactions, 2. the pathogen with partly isolate-specific differences (Darsow et al. 1988),

and 3. the living environment as phylloplane, micro flora on stems, roots and tubers. The influence of other micro organisms on reaction of the potato against late blight is insufficient investigated (Fox 1981) and includes potential of increasing defence (Schoenbeck et al. 1980, Hanson & Howell 2004, Buck 2004, Harman et al. 2004, Shoresh et al. 2005). *Mucor spinosus*, *Rhizoctonia solani* and *Trichoderma viride* had a lytic effect on *P. infestans* (Lacey 1965). It is known that in some regions tuber infections are rarely or unknown because of suppressive biotic and/or abiotic factors (Adrivon 1994, Garzon & Forbes 1999).

Particularly for assessing of quantitative resistance it is important to know the probable magnitude of the effect of single factors to consider it with nowadays better technical possibilities to preserve the chance of correct selection and successful breeding. Taking the test sample of leaves or tubers has to consider the variance within plants and between plants of the same potato clone. Results are not discussed in detail here, because a part is generally valid and a part depends from concrete conditions of each test date. That in substance means the necessary personal experience for successful application of methods for quantitative resistance. A main part of references is given in the following table 2 as help for quick information and as hint not to repeat in research what is known since several generations.

Table 2 Factors affecting quantitative late blight resistance and references

Age or physiological stage of potato plant/maturity: Kuehn 1871, 1880, de Bary 1876, Petermann 1891, Jones 1905, Appel 1917, Loehnis 1922, de Bruyn 1926a, b, Salaman 1926, Vowinckel 1926, Mueller 1930, 1931, Beaumont 1934, Crosier 1934, Rybin et al. 1947, Mills 1938, Gaeumann 1946, Huettenbach 1951, Schaper 1951, Grainger 1956, Black & Gallegly 1957, van der Plank 1957, 1963, 1984, Toxopeus 1958, Haussdoerfer 1959a, Lowings & Acha 1959, Hodgson 1961, Lapwood 1961b, Main & Gallegly 1964, Naumova 1965, Mooi 1966, Malcolmson 1969a, Takakuwa 1969, Umaerus 1970, Warren et al. 1971, 1973, Dowley et al. 1975, Umaerus & Lihnell 1976, Secka 1980, Carnegie & Colhoun 1980, 1982, Rotem & Sari 1983, Stewart et al. 1983b, Darsow et al. 1988, Stewart 1990, Singh & Bhattacharyya 1995, Gamboa et al. 2002, Visker et al. 2003a.
Leaf age, leaf position: Mueller 1931, Crosier 1934, Stelzner & Lehmann 1944, Huettenbach 1951, Mueller & Haigh 1953, Haussdoerfer 1959a, Hodgson 1961, Knutson 1962, Weindlmayr 1965, Malcolmson 1969a, Lapwood 1971, Warren et al. 1971, Umaerus & Lihnell 1976, Carnegie & Colhoun 1980, 1982, van der Plank 1984, Singh et al. 1999a, Visker et al. 2003a.
Age of tubers and its storage conditions: Zan 1962, Fehrmann 1963, Henriksen 1969, Boyd 1972, Barskaya et al. 1978, Chalenko et al. 1980, Darsow & Meinl 1981a, Stewart et al. 1983a, Darsow 1983a, 1987b, 1988a, 2004/5a, b, Bjor 1987, Bhatia & Young 1980, 1985, Grinberger et al. 1995, Lebecka et al. 2006, Kirk et al. 2010.
Injury of tubers before inoculation: Henriksen 1969, Ullrich 1970, Schoeber & Hoeppner 1972, Deahl et al. 1974, Smith & Rubery 1981, Darsow 1986.
Environmental conditions during host-pathogen interaction
Temperature during testing: Vowinckel 1926, Larance & Martin 1954, Haussdoerfer 1959a, Jeschke 1967, Royle 1976, Secka 1980, Harrison et al. 1994, Kirk et al. 2010.
Day length during testing on sporulation on leaves : Vowinckel 1926, de Weille 1963, Romero & Erwin 1969, Cohen et al. 1975, Goetz 1991b, Rubio-Covarrubias et al. 2005.
Light quality during test: Sakai (1961), Cohen et al. 1975.
Content of CO_2 in air during test: Zan 1962.
Atmospheric humidity on sporangia production on leaves during testing: Harrison & Lowe 1989.
Wind during testing of leaves: Harrison & Lowe (1989).
Environmental conditions of the host before host-pathogen interaction
Temperature during potato growing before testing: Crosier 1934, Ullrich & Krug 1965, Dorozhkin et al. 1972, Sato 1979, Secka 1980, Harrison et al. 1994, Spijkerboer et al. 1999, Rubio-Covarrubias et al. 2005, 2006.

Water supply of the plant before testing: Crosier & Reddick 1935, Vinogradova 1940, Johnson 1947, Ullrich & Krug 1966, Bychenkova 1973, Carnegie & Colhoun 1980, 1982, Darsow et al. 1988.

Soil type: de Bruyn 1922, Loehnis 1925, Dorozhkin 1955, Zeck 1957, Bychenkova 1976, Kolbe 1982/83.

Soil moisture before inoculation of tubers: de Bruyn 1926b, Grainger 1957, Zeck 1957, Monson & Eide 1964, Bychenkova 1973, Walmsley-Woodward et al. 1975, Henriksen 1978, Lapwood 1977, Stewart et al. 1993, Darsow 2004/5b.

Fertilization of potato plant: Wollny 1897, Hecke 1898, Laurent 1899, Vowinckel 1926, Schick & Lehmann 1936, Limasset 1939, Lepik 1939, Vinogradova 1940, Alten & Orth 1941, Hagenguth & Griesinger 1941, Kroener & Voelksen 1942, Koblet 1947/48, Haenni 1949, Malenev 1952, Awan & Struchtemeyer 1957, Black & Gallegly 1957, Popkova 1958, Lowings & Acha 1959, Gallegly & Niederhauser 1959, Kharitonova 1961, Birnbaum 1962, Langbein & Pehl 1962, Umaerus 1963, 1969b, 1970, Main & Gallegly 1964, Weindlmayr 1965, Mudich 1967, Borys 1968, Herlihy 1970, Szcotka et al. 1973, Umaerus & Lihnell 1976, Reichenbuch et al. 1977, Henriksen 1969, 1978, Dorozhkin & Panasevich 1979a, b, Stroykov et al. 1980, Bordukova & Ganzyan 1983, Rotem & Sari 1983, Stroinski et al. 1990, Rubio-Covarrubias & Gruenwald 2000, Colon et al. 2002.

Day length during plant growing: Vowinckel 1926, Vinogradova 1940, Kammermann 1951, Umaerus 1959, Weindlmayr 1961, 1962, 1964, Fehrmann 1963, Rothacker et al. 1964, Ullrich & Krug 1965, Bychenkova 1976, Darsow et al. 1988, Colon 1994, Harrison et al. 1994, Rubio-Covarrubias et al. 2005, 2006.

Light intensity before inoculation: Rothacker et al. 1964, Umaerus 1970, Bychenkova 1979, 1983, Victoria & Thurston 1974, Schumann & Thurston 1977, Darsow et al. 1988, Harrison et al. 1994.

Distance of plants: Songyn & Szysz, 1977, Carnegie & Colhoun 1980, Bordukova & Ganzyan 1983.

Year of growing and location: Kapsa 1980, Darsow 1987a.

Ontogenic factors

Influence of living environment on the potato-*Phytophthora infestans* interaction

Influence of the existing micro flora on and in potato tissues: de Bary 1876, Murphy 1922, Gradinaroff 1943, Peterson 1943, Schultz 1952, Zan 1962, Lacey 1965, Hollomon 1967, Bainbridge & Dickinson 1972, Sturdy & Cole 1974, Schoenbeck et al. 1980, Sidhu 1980, Fox 1981, Campbell 1989, Andrivon 1994, Clulow et al. 1995, Garzon & Forbes 1999.

Infection with other pathogens: Quanjer 1913, Mueller & Munro 1951, Richardson & Doling 1957, Bliznets 1969, Mitsene 1970, Singh et al. 1970, Pietkiewicz 1971, 1974, 1975, 1977, Wood et al. 1971, Dowley 1973, Stroykov 1974, Borisenok & Pershutina 1974, Khramcova & Zetsyukin 1975, Fernandez de Cubillos & Thurston 1975, Schoeber & Bode 1975, Volovik & Komkov 1975, Komkov 1976, Novakova 1977, Kremnyova & Grebenshchikova 1978, Lytayeva & Ligay 1978, Dzhalilov 1982, Shmyglya & Dzhalilov 1983, Schoeber & Weidemann 1982, 1984, Kalra et al. 1988, Darsow & Wulfert 1989a, b, Raya-Serrano & Lozoya-Saldaña 2006, Kelly et al. 2006.

In some circumstances physiological plant stage was interpreted to be effective, caused by different fertilization (Reddick 1928a, Mills 1938, Limasset 1939). A part of different behaviour from young to old plants in the field can be explained by different microclimate in the crop (Johannes 1953).

As expected, differences were found in comparison of quantitative resistance reaction under greenhouse and field conditions on foliage (Huettenbach 1951, Mueller & Haigh 1953, Hausdoerfer 1959a, Gallegly 1962, Knutson 1962, Malcolmson 1976, Tschanz 1978, Nilsson 1981, Caligari et al. 1984, Colon 1994, Douches et al. 2002b, Andreu et al. 2010) as well as on tubers (Pietkiewicz 1977, Douches et al. 2002b). At CIP, Lima, foliage blight incidence of seedlings correlated with adult plant attack r = 0.58 (Anonymous 1989). For breeding it is to estimate, which advantage brings selection with cultivation in greenhouse, how large is the difference of host reaction in both conditions and can the part of wrong decisions been tolerated (see table 3). One has to consider that the clone x environment interaction constitutes a part of genotypic resistance behaviour, which is distinctly expressed on only a part of genotypes and means that quantitative resistance is most correctly evaluated in conditions similar to the field conditions in which the crop will be grown (Buddenhagen 1981). Today potatoes are grown in 149 countries from latitudes 65°N to 50°S and altitudes from sea level to 4000 m (Hijmans 2001). In case of more standardized cultivation in greenhouse, only the part of clones with low(er) reaction on environmental conditions will show similar reaction in the field. Usually, a part of the highly susceptible and of highly resistant ones are lesser influenced by the environment.

In comparison of seedlings selection for foliage blight resistance in greenhouse to results of field assessment environmental and ontogenic differences, both may be effective together. Table 3 shows examples for extreme differences too (unpublished results of experiments of Darsow 1992a, b). The variability of quantitative late blight resistance is one of the crucial points for potato breeding progress in resistance. However, with assessment of resistance is intended to give a forecast of the resistance behaviour for particular growing conditions, which vary in a range of environmental and other conditions. Its most influencing factors should therefore in a part of that range vary in several tests too and not be excluded by standardization.

Table 3 Foliage and tuber blight resistance of pre-breeding material of ZL Gross Luesewitz as seedling under greenhouse conditions and in field assessment for foliage blight as well as tuber blight resistance in tuber slice test. Increased resistance is scored 1-9. Examples out of 838 individuals are given assessed as seedlings and clone in the field (average of two years) assessment.

	Foliage blight resistance		Tuber blight resistance		Resistance on	
Clone	Seedling	Field	Seedling	Field	Foliage	Tubers
6301.06	≤ 3.0	1.5	2.0	2.6	equal	equal
6295.149	≥ 8.0	8.2	7.2	7.0	equal	equal
6308.32	≥ 8.0	8.7	8.5	8.9	equal	equal
6310.520	≥ 8.0	7.2	3.3	2.3	similar	similar
6308.20	≥ 8.0	7.5	3.3	3.1	equal	equal
6295.38	≤ 3.0	2.8	7.1	7.7	equal	similar
6194.143	≤ 3.0	3.5	7.3	8.4	equal	similar
6295.33	≤ 3.0	3.2	3.0	6.2	equal	very different
6295.06	≤ 3.0	1.4	4.1	7.7	similar	very different
6308.191	5.0	4.5	6.8	5.6	equal	different
6308.225	5.0	3.2	6.5	5.9	different	similar
6297.139	≥ 8.0	8.0	7.3	5.1	equal	different
6310.497	≥ 8.0	7.7	7.8	5.5	equal	different
6297.127	≥ 8.0	7.7	3.8	6.8	equal	very different
6297.122	≥ 8.0	6.9	3.5	7.5	different	very different
6194.88	≤ 3.0	5.1	3.0	1.8	different	similar
6194.108	≤ 3.0	6.0	2.0	3.4	very different	different
6295.13	≤ 3.0	7.7	6.1	7.6	very different	different
6194.183	5.0	7.9	6.2	8.6	very different	different
6310.485	≥ 8.0	3.0	2.5	3.9	very different	different
6310.661	7.0	1.4	2.5	2.5	very different	equal
6310.718	7.0	1.8	6.7	7.1	very different	equal
6310.484	≥ 8.0	1.3	6.9	8.2	very different	different
6295.29	≤ 3.0	8.4	4.5	8.1	very different	very different
6295.28	≤ 3.0	5.9	2.5	6.2	very different	very different
6194.88	≤ 3.0	5.4	4.6	1.8	very different	very different
6305.35	7.0	2.6	1.2	6.8	very different	very different
6295.151	≥ 8.0	1.9	1.8	5.7	very different	very different
6303.98	≥ 8.0	4.6	5.5	2.8	very different	different
6308.122	7.0	3.8	7.0	4.2	very different	different

Concerning tuber blight a part of differences in table 3 is determined by methodical differences (test of seedlings tubers and tuber slice test). In foliage blight, age of the plants makes probably the main part of the differences. The data show the possible level of changing in both directions in comparison of young and adult plants. Methodical errors were excluded as far as ever possible. Consequence for applied methods will be discussed later (chapter 4 and 6).

There is less reason to expect lower losses by late blight in future due to change of climate because the disease can occur over a range from about 5°C to 30°C; the pathogen survived temperatures of 40°C in stem tissue (Kable & Mackenzie 1980, Flier 2001). More rapid spore germination stated Flier (2001) for the Netherlands populations with warming. Sporangia could regain viability after drying if rehydrated gradually (Minogue & Fry 1981). Only a short period of suitable conditions is required for haulm destruction, more than 100 000 sporangia can be produced from a single lesion (Forbes & Landeo 2006). Different components of resistance may be differently affected by climatic conditions during the pre-inoculation period. A month growing at 24°C resulted in higher AUDPC than at 16°C (Rubio-Covarrubias et al. 2005). Penetration frequency was found to be higher at 24°C than at 16°C (Rubio-Covarrubias et al. 2006). A little increased temperature may shorten the generation time of *P. infestans*. Occurrence of more extreme weather situations are connected with hindrance of oomycide application in periods of highest demand. Prolonged vegetation period in northern parts of temperate climate will increase the incidence of late blight there (Hijmans 2001, Hannukkala 2011). Milder winters with less frost lead to increased number of tubers that survive as ground keepers and will emerge, thereby acting as a source of inoculum and multiplication for *P. infestans* early in the season, of nematodes and other pathogens and pests too (Haverkort & Verhagen 2008).

In spite of effects of leaf position, plant age, tuber age and cultivar-specific reaction on environmental factors crop physiology can only little contribute to reliably reduce the losses caused by *P. infestans* in potato production. For instance, advancing tuber bulking by manipulating the physiological age of the seed tubers should increase tuber yield before late blight incidence. However, at the same time this treatment influences emergence, early vigour, canopy structure, rate of tuber bulking and leaf senescence; its overall effect is difficult to predict (Struik 2010).

2.5. The term resistance in context of foliage blight as mixed effect of true resistance and physiological potato stage or maturity

In principle, the potato plant can be blighted in each stage of its development, but there are differences in probability to become ill due to other additional factors. The designation late blight for the foliage disease caused by *P. infestans* is deduced from its common appearance after flowering under European conditions at the 19th century (Mueller & Haigh 1953). Under long-day conditions early potato cultivars usually are firstly attacked by *P. infestans* (Petermann 1891). Since more than 120 years severity of foliage blight has been directly used as measure of resistance, although it was known that physiological stage (maturity) of the potato clone has a higher effect than polygenic determined resistance on the disease level (Mueller 1930, 1940, 1949, 1953, Salaman 1931, van der Plank 1957, 1963, Toxopeus 1958, Lapwood 1961b, Main & Gallegly 1964, Takakuwa 1969, Umaerus et al. 1983), and vegetation of potato clones takes between 70 and about 200 days for most early to very late material (Schick & Hopfe 1962). A correlation coefficient of r = 0.71 was calculated between maturity and late blight of foliage by Zadina (1966), of r = 0.85 by Colon et al. (1995a), and of r = 0.81 by Rahkonen et al. (2006). Mueller (1940) and Schick et al. (1958b) named most very late clones fictitiously resistant (in German: scheinresistent). Delayed crop development with unfavourable microclimatic conditions postpones incidence. Salaman (1931) traced back delayed blight incidence of cv. Champion to its lateness only.

That ignoring, the level of disease of potato clones is equated with their resistance independent from maturing stage. This simple conclusion is largely appropriate and common for quali-

tative resistance as decision between sporulating lesions or not sporulating reaction, but is all wrong for quantitative resistance under long-day conditions, which has to be separated from the ontogenic effect. Already Mueller (1930) and Salaman (1931) argued against wrong conclusion from incidence to resistance level. Multidisciplinary cooperation would have been necessary, but besides pathology physiology and breeding were not involved in development of assessment methods for quantitative foliage blight resistance for more than 100 years. Therefore earliness is correlated with "susceptibility" and lateness with "resistance" (Toxopeus 1958, Umaerus et al. 1983, Swiezynski 1990, Ewing et al. 2000, Visker et al. 2004, Visker 2005, Haynes et al. 2007b, Struik 2010) in the whole literature up till now with very few exceptions. On this base Maris (1962) assumed that "resistance" and lateness are probably pleiotropic effects of genes connected with control of photoperiodic reaction. Consequently the most significant quantitative trait locus for foliar "resistance" across three environments was mapped in the same position as late maturity (Gebhardt 1999, Collins et al. 1999, Visker et al. 2002, Visker 2005). Ewing et al. (2000) found several QTL for foliage blight resistance in regions of the genome to which QTL's for late maturity have previously been mapped. Simko et al. (2007) summarized the current state of knowledge in following: "However, the most resistant cultivars are also late-maturing, and it is not known whether durable resistance can be combined with early maturity." How should another result occur from the base of mixed trait?

Common use of the term foliage resistance to late blight in research and breeding up till now – with very few exceptions - is based upon the described inadequate method of assessment.

Consequences are:

1. Use of partly insufficient sources of resistance (lateness masks susceptibility or insufficient resistance) often results after long time in breeding material only for discarding, because breeding for quantitative late blight resistance becomes breeding for lateness or R-genes in opposite to the strategic aims to combine it with earliness and quality.

2. Molecular research detects QTL for "resistance", which are not identically with gene locations of true resistance, and recommended these for marker-assisted selection.

3. Breeders underestimate the potential of polygenically determined resistance according to their disappointing experience, do not start with it or finish its preliminary attempts and hope on gene technique.

4. Diversity of *P. infestans* populations and its dynamics is not correctly registered in the ratio of virulence genes because of interfering high maturity differences between differentials commonly used.

For breeding purpose one has to separate the effect of maturity on blight incidence to obtain quantitative foliage blight resistance. Whilst Toxopeus (1958, 1959) did not belief that quantitative foliage resistance to *P. infestans* and earliness can be combined, Schick et al. (1958b) found different levels of quantitative resistance in all maturity groups. Frandsen (1958) argued that both traits are combinable. Umaerus (1969b) did not find a narrow correlation between resistance and maturity in breeding material descended from *S. demissum*. Mueller (1951) mentioned that for instance, very late cv. Wohltmann was wrongly characterized as blight resistant. Only at ZL Gross Luesewitz both traits were separated in pre-breeding practice since decades with impressive, but slow progress in utilization of minor gene resistance from diverse wild potato species (Darsow 1989b, c, 1991b, 1999, 2002a, b, 2003b, 2005a, 2008). Most German breeders calculate the resistance meanwhile with a new procedure in opposite to selection according to blight incidence as rAUDPC (Darsow & Strahwaldt, not published, Truberg et al. 2009). For more discussion see 4.2.4.

In monitoring of *P. infestans* populations the extreme lateness of Blacks differential R9 (clone 2573[2]) combined with quantitative resistance results in very few or very late incidence in Europe and in Mexico too (Lozoya-Saldaña et al. 2006). Therefore its foliage blight level is not

comparable with other differentials in long-day conditions at the same date. The frequency of virulence gene vir 9 in the late blight population is usually underestimated and its value as potential source of R-gene resistance is usually overestimated due to the lateness effect as for instance in case of Hannukkala et al. (2005), Sliwka et al. (2006b) and Cooke et al. (2011a). A bit lesser is the lateness effect of differential R8. Own experience corresponds to described results of sporulating in moist chamber, but long time not in the field (Cooke et al. 2011b). A breeder should further develop the set of differentials to a better comparable level concerning its maturity, growing habit, the quantitative late blight resistance level and the facility visually to diagnose virus infections. For practical purposes inclusion of new R-genes would be desirable.

Moeller and Reents (2007) did not find an advantage of "foliage blight resistant cultivars" compared with susceptible ones in organic farming, because delayed incidence of foliage was connected with delayed tuber growth; it means "resistance" was only a maturity (lateness) effect.

The same problem of negative association between earliness and resistance exists in potato/*Alternaria solani* (Santa Cruz et al. 2009).

On potato tuber blight the correlation between lateness and resistance is lesser expressed (Toxopeus 1958, Mooi 1970). According to own experience lateness had the tendency of increased susceptibility, which would make sense in coevolution of host and pathogen in view of owerwintering of the pathogen.

2.6. State of research on pathogenicity of *P. infestans* (Mont.) de Bary, considering mainly quantitative pathogenicity

Central Mexico is assumed to be the centre of origin of the late blight causal agent with the longest co-evolution of pathogen and host, and the region with the highest genetic diversity of the pathogen (Reddick & Crosier 1933, Reddick 1943, Graham et al. 1959, Budin 1970, Rivera-Pena 1990c, Niederhauser 1991, Andrivon 1995, Flier et al. 2003b). The pathogen has the ability to manipulate biochemical, physiological and morphological processes in the host plants through so called effectors, which suppress defence responses in compatible host-pathogen relation. The genome of *P. infestans* with 240 Mb is sequenced and should later provide insight into key molecular processes regulating quantitative pathogenicity too (Kamoun 2002, Haas et al. 2009). 17,797 protein-coding genes are predicted for *P. infestans*; its genome showed an extremely high repeat content and unusual discontinuous distribution of gene density. Gene-dense regions with conserved gene order are interrupted by repeat-reach expanded regions that are sparsely populated with genes, many of which are fast evolving pathogenicity effectors such as the RXLR and CRN families (Haas et al. 2009). 494 genes were induced at least twofold during infection with *P. infestans* relative to mycelial growth, among those 79 RXLR-genes and few very highly expressed CRN-genes; 115 genes were down regulated (Haas et al. 2009). However, research to the function of these single genes and its interaction has mainly to start in future (Goodwin 1991, Pieterse et al. 1992, Govers 1999, Whisson et al. 2005, Haas et al. 2009). Some dominant avirulence genes are mapped (van der Lee 2001). Thousands of sequenced cDNAs from *P. infestans* and potato are housed in the *Phytophthora* Genome Initiative database (Waugh et al. 2000). Novel necrosis inducing cDNAs were detected (Torto et al. 2003).

The known four mitochondrial types of *P. infestans* are sequenced with a size between 37,922 and 39,870 base pairs. Among these haplotypes 81 mutations were detected (Avila-Adame et al. 2006). The results support continuation of discussion about the importance of the Andean region in the evolution of *Phytophthora* species.

Phytopathological data on European populations of *P. infestans* are available in the EUCABLIGHT database using a PC-program 'Phytophthora.exe' in www.eucablight.org (Cooke et al. 2006, 2007, Hansen et al. 2006a). Information about aggressiveness, virulence, mating type, Metalaxyl resistance, mtDNA, AFLP-, Isozyme- and SSR-markers are given over years, countries, and regions. Cooke and Lees (2004) summarised information about markers for *P. infestans*.

Already de Bruyn (1947) regarded *P. infestans* as very plastic and adaptable pathogen, which is characteristically especially for biotrophic and hemibiotrophic airborne oomycetes and fungi (Parlevliet 1993). Minor gene effects of quantitative pathogenicity are very difficult to discriminate and therefore their number, its mechanism and its inheritance are mainly unknown. "To date, hardly anything is known about the molecular basis underlying pathogenicity of *P. infestans*" wrote Pieterse et al. (1992). The sexual and asexual population are not generally different concerning its pathogenic fitness (Person et al. 1976, Tooley et al. 1986, Fry & Spielman 1991). The question seems if production of oospores enables a quicker changing. High pathogenic variability in asexual populations of *P. infestans* is explained by migration (Goodwin et al. 1994), mutation (frequency 10^{-7} to 10^{-8}, Parlevliet 1976, Engel 1980), heterokaryosis (Parmeter et al. 1963, Dyakov & Kulits 1978), and anastomosis, fusion of zoospores, parasexuality (Tinline & Mac Neill 1969), mitotic crossing-over, cytoplasmatic control or somatic recombination (Gallegly 1970, Denward 1970, Dyakov & Kulits 1978, Shaw 1983, Shaw & Shattock 1991, Al-Kherb et al. 1995). Heterokaryons and heterozygous diploids have been reported by Kulits & Dyakov (1979). Hyphal anastomosis may be a mechanism for exchange of genetic material (Gaeumann 1946, Wilde 1961, Malcolmson 1970, Goodwin 1997). Fusion of zoospores (Gallegly & Eichenmueller 1959) and zoospore-mediated hyphal fusions are obtained with mixed cytoplasm (Judelson & Yang 1998). Somatic recombination has been occurred in the unsepted mycelium (Leach & Rich 1969, Denward 1970). Caten and Jinks (1968) observed about 5% of zoospores with more than one nucleus. Single zoospore-isolates from asexual PI-105 differentiated into 14 races (Abu-El Samen et al. 2003). Poedinok et al. (1982) obtained evidence of mitotic crossing over in the parasexual cycle of *P. infestans.* Diploid nuclei arise within heterocaryons (Pipe et al. 2000), crossing over between homologous chromosomes may occur, and gradual haploidization occurs by nondisjunction, yielding haploid recombinants (Kuhn 1991). New expressions of virulence arising from avirulent isolates may be the result of mutation (Samsone 1940), but more often of rearrangement or isolation of recessive alleles previously present within a heterozygous genome (Le Grand-Pernot 1988). Vegetative incompatibility groups were found among isolates of *P. infestans* in Russia (Goroborova et al. 1989, Anikina et al. 1993). Isolates from central Mexico are almost exclusively diploid, whilst outside of Mexico mainly tetraploid and aneuploid isolates coexist in the field (Sansome & Brasier 1973, Sansome 1977, Tooley & Therrien 1987, 1991, Daggett et al. 1993, Carter et al. 1999, Singh et al. 1999b). The factors influencing the ploidy level are not known (Fry & Spielman 1991). Since polyploids can harbour a wider array of virulent allele combinations compared with diploids, polyploidy could contribute to the development of the many virulence phenotypes observed (Sansome 1977) and similarly to changing of aggressiveness level.

Oospore formation (Clinton 1911) as result of sexual reproduction and most intensive source of genetic diversity (Niederhauser 1991, Rivera-Pena 1995) of the heterothallic *P. infestans* has been observed in the field of many countries (Goetz 1991b, Drenth et al. 1995, Forbes & Landeo 2006). Its longevity and potential for increased pathogenicity strengthened the global danger from blight. Most virulent races of *P. infestans* are found in regions with A1 and A2 mating type in similar ratios as in Toluca and Chapigno region of Mexico with abundant oospore production (Galindo & Gallegly 1960, Rivera-Pena 1995). Beyond that oospores may be formed by selfing (from heterocaryons, Shaw & Shattock 1991) or in response to stimulation by other species of *Phytophthora* or by quite unrelated microbes and the events of such oospore development have been increased compared to past (Fry & Smart 1999). The oospore development seems to be stimulated by cold periods (Hermansen et al. 1999), or by some fungicides (Trout & Ristaino 1999). A trisomic nucleus carrying both A1 and A2 determinants could yield a heterocaryon with some nuclei carrying a single determinant by chromosome loss or crossing over during mitosis (Shaw 1991). Van der Lee et al. (2004) hypothesized that trisomy and subsequent instability of chromosomal regions or loss of complete chromosomes significantly contribute to the notorious genetic flexibility of *P. infestans*.

Qualitative pathogenicity is governed by genes for avirulence/virulence. Avirulence alleles are dominant and virulence alleles are recessive (Shaw 1991, Al-Kerb et al. 1995), however other hypothesis of inheritance are discussed too (Erwin & Ribeiro 1996). Shattock et al. (1986) assumed pathogenicity generally to be inherited recessively. Resistance to metalaxyl (oomycide) is chromosomal inherited by a single exhibiting incomplete dominance (Shattock 1988). Resistance to some antibiotics are inherited via extra chromosomal cytoplasmatic control (mitochondrial DNA) and would thus be inherited only through the maternal parent. Quantitative pathogenicity is probably determined by multiple genes that are complexly inherited, thus making phenotypes of progeny from segregating populations difficult to interpret (Erwin & Ribeiro 1996). A study of quantitative aggressiveness on leaves in sexual progeny showed 15-19% non-pathogenic individuals and 6-22% more aggressive than the most pathogen parent (Earnshow & Shattock, 2002). Quantitative fitness factors as well as mycelium growth rate as quantitative pathogenicity are assumed to be under cytoplasmatic control (Caten and Jinks 1968, Caten 1970). Four variant forms of mitochondrial genome are described by Goodwin (1991). Caten (1970) found positive correlations between intensity of sporulation and growth rate in tubers (r = 0.755) as well as between growth rate on leaves and tubers. Serine protease activity of mycelium extract was found to correlate with aggressiveness of isolates in detached leaf test (r=0.73, Hamill et al. 2006). The components of quantitative tuber pathogenicity studied were not correlated to quantitative foliar pathogenicity factors, as measured under growth chamber conditions (Flier et al. 1998). This additionally supports resistance in foliage and tuber to consider as different traits in breeding. Increased aggressiveness of new isolates on tubers than displaced, pre-existing ones stated Peters et al. (1999).

Flier and Turkensteen (1999) calculated a composite aggressiveness index AI by multiplication of latent period LP10 with speed of appearance of maximal number of sporulating disks (MGR), infection efficiency (IEI) and spore number per cm^2 (SP), $AI = 1/(LP10 \times MGR \times IEI \times SP) \times 10^4$. The following relations between the components were found (table 4). The use of 14 mm leaf disks restricted evaluation of sporulation capacity, for methodical details see chapter 4.1.7. Only the number of blighted disks and speed in reaching first 10% and its maximal number could be differentiated.

Table 4 Spearman rank correlation coefficients r of aggressiveness components of 36 isolates of *P. infestans* on leaf disks of Bintje according to Flier and Turkensteen (1999). LP10: generation interval, MGR: speed to reach maximal number of blighted disks, IEI: infection efficiency index, SP: sporangia produced per cm^2, AI: aggressiveness index.

Component	LP10	MGR	IEI	SP
MGR	-0.33*			
IEI	-0.61**	-0.81**		
SP	-0.12	-0.14	-0.13	
AI	-0.55**	0.95**	0.93**	0.17
Mating type	-0.11	-0.01	-0.03	-0.19
Virulence gene number	0.16	-0.04	-0.05	-0.34*

The occurrence of sexual reproduction of *P. infestans* in the field has been reported for North America, Europe and other parts of the world caused from potato export from Mexico between 1976 and 1978 (Deahl et al. 1991, Drenth et al. 1993, 1995, Niederhauser 1991, 1993), but its real importance in the new populations is under discussion for instance for Europe (Fry et al. 1993,

Sujkowski et al. 1994, Fry & Smart 1999, Shaw & Wattier, 2002, Andrivon 2005, Griffin et al. 2005, Cooke et al. 2007). Great regional differences occur (Elansky et al. 2001, Cooke et al. 2011a). Day and Shattock (1995) found that new populations were not significantly more aggressive (quantitatively pathogen) than old isolates, but more virulent (qualitatively pathogen). However, on Sakhalin only A1 was found with higher virulence gene combinations than in other Russian regions with more genetic diversity and both mating types (Elansky et al. 2001). Genetic diversity of *P. infestans* in the Netherlands seems 10fold higher than in UK (Shaw & Wattier 2002), however, a clonal lineage of A2 (blue 13) increases in Europe since 2005 which appears to be more aggressive than resident pathogen genotypes (Cooke et al. 2007, Kildea et al. 2011). The higher aggressiveness of isolates 6_A1 and 13_A2 was mainly expressed in the components generation interval and sporulation capacity on cvs. Sarpo Mira and Bionica (Nyongesa et al. 2011). Using one of both for reassessment of foliage blight resistance of 50 cultivars for the Potato Council Ltd has revealed significant shifts in the rating of many cultivars to be more susceptible and has confirmed good level of some (Carnegie et al. 2011). Gardens, allotments and fields with potatoes each or each second year are most probably locations of highest diversity, of sexual reproduction and earliest disease occurrence. Oospore production is determined more by general combining ability of the mating strains than by specific combining ability; presence of sexual incompatibility or lethal factors are found (Flier 2001). Genetic drift seems to eliminate most new genotypes of the pathogen; only such, adapted for survival from season to season in seed or dumped or volunteer tubers go on as perennial genotypes (Shaw & Wattier 2002, Thompson & Cooke 2005). It is surely, the agro-ecosystem promotes survival and propagation of new genotypes of the pathogen compared with wild habitat (Gruenwald et al. 2001).

Migration by global potato trade has been intensified. Migration and mutations are shown in its importance for current Japanese late blight population (Akino et al. 2011). It seems that population development of *P. infestans* includes adaptation to a wider range of temperature (Mizubuti et al. 2002), which is connected with increased epidemiological potential. High diversity and increased aggressiveness is found currently (Cooke et al. 2007). Andrivon (1998) pointed out that single components of aggressiveness do not always directly correlate with its pathogenicity at all. Whilst cultivars influenced the development of isolates cultivar-specific after mixed inoculation on the field in North Ireland, such interaction did not occur in Michigan, USA (Young et al. 2007); the interaction cultivar x isolate could not be explained by the level of aggressiveness. Andrivon (2005) did not find significant differential adaptation of isolates to cultivars in a region of France.

In literature often is registered that most complex virulent races are detected late in the season with regional and yearly differences (Mastenbroek & de Bruyn 1955, Toxopeus 1956a, 1961, Schick et al. 1958a, Kameraz 1964, Popkova & Stroykov 1977, Rivera-Pena 1990b, Zarzycka et al. 2000, Lozoya-Saldaña et al. 2005). It is open if increased virulence came into being by mutation from more simple ones during vegetation period or mainly from infected seed tubers (with the best fitness for overwintering). However, if development by mutation yearly would happen then some R-genes in varieties should support resistance at the beginning of the season. Changing of quantitative pathogenicity may happen too by mentioned mechanisms and as result of pathogen/environment interaction, but with lesser consequences than mutation in avirulence loci (Denward 1970, Gallegly 1970, Parlevliet & Zadoks 1977). A relative specialization of *P. infestans* to tomato or potato exists with partly aggressiveness to both hosts (Legard et al. 1995, Andrivon et al. 1998). It seems that outside North America isolates do not have the genetic potential for developing high levels of aggressiveness on both hosts potato and tomato (Forbes et al. 1996).

Environmental influence on quantitative pathogenicity of *P. infestans* occurs similarly as on the host (Yarwood 1962, Johnson 1993), for instance of season (Sujkowski et al. 1986a, b), of temperature (Larance & Martin 1954), of light quality (McKee 1969, Cohen et al. 1975, Dyakov et al. 1975), day length (Cohen & Rotem 1970), atmospheric pressure and radiation (Bortels

1951, Bortels & Massfeller 1963), acidic level (Huettenbach 1951, van Bruggen et al. 1987), ion concentration (Okorokov et al. 1976). However, little research is conducted about it (Lehmann 1938a, Harnish & Barnett 1962, Yarwood 1962, Henniger 1966, Royle 1976, Tverskoy et al. 1981a, Grand-Pernot 1981, van der Plank 1982, 1984). Unexpected short-term deviate from the normal pathogenic level in partly standardized condition may be explained that way.

2.7. State of breeding research for quantitative late blight resistance of foliage

2.7.1. Aspects of breeding

Breeding for resistance is known in several ways: conventional breeding, population breeding, mutation breeding, using of somaclonal variation. Methods of incorporating resistance are sexual hybridization, somatic hybridization, asymmetric fusion, gene transfer by gene technique. Details are debated in chapter 5.2.-5.6. Breeding clones and most cultivars possess the genome of *S. tuberosum* ssp. *tuberosum* (*tbr*) with fragments from other *Solanum* species. Somaclonal variation became apparent as limited useful method to increase variation in breeding and is summarized by Umaerus and Umaerus (1994).

Tetrasomic inheritance of the potato is difficult to interpret (Bradshaw 2007b), above all expression of quantitative traits of potato is difficult to understand because of several reasons: the tetraploid nature of the potato genome, which is not simple autotetraploid (Bradshaw 1994, Wilkinson 1994), the high degree of heterozygosity, the absence of homozygous inbred clones, the frequency of distorted segregation ratios (Black 1947, Hermsen 1994), the number of included genes, it's frequently small effect, the gene/environment interaction (Bradshaw 1994). Additional factors of variability act from the side of the pathogen (aggressiveness, virulence, ploidy, it's interaction with environmental factors). Permanent changing environment (temperature, moisture, light intensity and duration, and other) influences the result of ontogenic regulated gene expression (Willmitzer 1987) and of host-pathogen interaction.

Literature on the environmental interaction on quantitative resistance is given in chapter 2.4. The probable magnitude of the effect of single factors may not be generalised because of difficult to predict multifactorial interactions. Moisture and temperature during the test, day length and light quality before the test may be the most important factors in testing foliage blight resistance. Fertilization, leaf position and its interaction with potato clones tested is described by Umaerus & Lihnell (1976). Year, location, greenhouse are complex conditions with different critical factors. Genotype-environment interaction components in potato trails are frequently the same order of magnitude as the genotypic differences; this limits the gain from heritability estimated in a single environment (Bradshaw & Mackay 1994). Such interactions complicate estimation of resistance inheritance and selection in breeding. Different ranking of clones in different environments is a common experience of each breeder in foliage blight assessment as it was found by Gans (2003). Significant interactions genotype x location and genotype x season and other are to known before selection. Therefore assessment in several years is necessary (3-4 years according to Yashina & Erochina 1977). More stable reacting potential cross parents are recommended to prefer (Mulema et al. 2004/05). The difference of experimental and expected reaction of standard clones informs about suitable management of environmental conditions before and in assessment of resistance.

The mechanism of quantitative late blight resistance is largely not understood (Friend 1991, Parker et al. 1991, Wastie 1991, Coffey & Wilson 1996, Schmelzer und Gus-Meyer 1998, Swiezynski & Zimnoch-Guzowska 2001, Parlevliet 2002, Bormann et al. 2004). Prell & Day (2001) wrote: "The mechanisms of race-non-specific resistance and how its expression is regulated, is largely

unknown because the contribution of each of the participating minor genes to the overall horizontal resistance is very small and difficult to identify and quantify." To discern small differences, good screening and assessment methods are necessary. Interplot interferences, earliness, tallness, and irregular distribution of inoculum often give rise to confounding effects in practice (Parlevliet 1993). The recognition and incomplete defence of the pathogen by its host implies a complex, dynamic communication network between both. First results with quantitative foliage blight resistance showed that the induction of biochemical response pathways of potato required up- or down-regulation of 143 genes 72 hours post inoculation, of which 35 genes were strongly induced (Ros et al. 2004). The gene induction is expected to be not only caused as a direct reaction to the pathogen, but as an indirect response to wounding by the growth of hyphae within the leaf. The energy metabolism and production of signalling proteins were more intensified in the moderate resistant cultivar than in the susceptible one (Ros et al. 2004). In the diploid population PD 24 loci were associated with foliage blight resistance: genes related to phenylpropanoid pathway, to chalcone isomerase and synthase, to WRKY regulation, to osmotin, and to cytochrome P450 (Trognitz et al. 2002). Quick progress can be stated in research on molecular level. The 840 Mb genome of potato has been sequenced from a diploid and a doubled monohaploid clone by a global consortium (Visser et al. 2009, Bryan 2010). The structural data has to be associated with its function in the biological system, a most difficult challenge concerning quantitative traits. One preliminary potato functional map of pathogen resistance can be seen, for instance in the PoMaMo database (https//gabi.rzpd.de/PoMaMo.html).

Active defence reactions require recognition of the pathogen as non-self and consequent signal transduction to activate the different defence responses. The molecular events are difficult to study in the interacted plant, since most processes of a successful resistance reaction happen in only a few cells at the site of infection. Cultured cell systems have been used to study the molecular biology of defence responses and mechanisms of pathogen recognition and signal transduction (Parker et al. 1991). Because of its nature research on other than quantitative resistance types (hypersensitivity and non-host reaction) are easier to understand and therefore preferred dealt with (96% according to Robinson 1973, Kamoun 2006, Verweij et al. 2011a); about 40 single dominant genes conferring qualitative resistance of potato have been positioned on the potato molecular map (Bradshaw et al. 2006a, Simko et al. 2007); 31 different R-genes to *P. infestans* are listed by Hein et al. (2009), 20 other than from *S. demissum*.

Nutritional-physiological differences often are assumed as reason of quantitative differences in late blight attack (Grainger 1956); however, for resistance breeding usable traits for indirect selection were found neither among carbohydrates and proteins nor among secondary metabolic products (Henniger 1966, Hohl 1991). Several substances were tested to be suitable for indirect selection for quantitative blight resistance as the content of glucane, phenols, ethylene synthesis after infection and pathogenesis-related proteins (PR-proteins). None of these and other factors proved to be suitable for indirect selection to resistance in breeding practice (Umaerus et al. 1983, Wastie 1991, Rubio-Covarrubias et al. 2006). Vleeshouwers et al. (2000a) found no correlation between basal PR mRNA levels and resistance at the genus level, but in intraspecific comparison of five selected cultivars of *S. tuberosum* ssp. *tuberosum,* three clones of *S. microdontum* and two clones of *S. sucrense* both were significant correlated. Several genes from the phenylpropanoid pathway were found to be associated with quantitative foliage resistance of South American diploid wild potato clones and a BC3-clone (Wullf et al. 2002). A host-encoded xyloglucan-specific endoglucanase inhibitor protein may contribute to non-R-gene mediated foliage blight resistance (Jones et al. 2005, 2006).

Tissue-specific expression of resistance is recorded for cotyledons and leaves of the same plant (Black 1952), leaves and tubers (Mueller 1928, Bonde et al. 1940), stables and leaves (Mueller 1950a, Lammers et al. 1998, Kapsa 2002b), inner and outer stem parts (Mueller 1950b), leaves and petals (Mueller 1950a, Porter et al. 2004), pith and cortex of tubers (Pathak & Clarke1987).

Because of small effects of unknown number of involved genes, its detection by classical genetic analysis is very difficult. Independent minor genes, modifiers and genes with other function (background genes) may contribute to the quantitative defence (Hassebrauk & Roebbelen 1975). In the EU project BIOEXPLOIT gene bank material was tested to identify QTL for quantitative foliage blight resistance on chromosome IV, V and X with new SNP markers besides major genes (Hoekstra 2009). Candidate genes associated with quantitative resistance are currently tested for their diagnostic power in marker-assisted selection experiments (Gebhardt et al. 2010). This work is most complicated and needs a lot of additional research to enable effective support of practical selection. It is expected that genetic engineering of quantitative blight resistance genes is still far away (Zadoks 1993). Stacking of minor resistance genes to combat late blight instead of pyramiding major genes "is not really an option as this will not result in a resistance level which is high enough" (Goverse & Struik 2009). This remark corresponds to common prejudice, but is realistically for current insufficient knowledge of minor genes. However, helpful tools support scientific progress (Tecle et al. 2010, Gebhardt et al. 2011).

Already Salaman (1931), Stevenson et al. (1937) and Bonde et al. (1940) explained the quantitative foliage blight resistance of potato to *P. infestans* as recessively inherited due to multiple genes. Polygenic inheritance is commonly accepted (Graham 1963, Abdalla 1970, Black 1954, 1970, Umaerus 1970, Thurston 1971). Transgressive inheritance is found which resulted in some seedlings of progeny (6-11%, Kirsanova et al. 1989) exceeding the most resistant parent (Lehmann 1938a, Montaldo and Akeley 1946, Frandsen 1958, Graham 1963, Budin & Soboleva 1982, Yashina & Simakov 2000). Also negative combining ability for blight resistance was observed in dihaploid fusions by Rasmussen et al. (1999), in crossing populations by Visker et al. (2004). Only few classical genetic studies of "inheritance of quantitative late blight resistance" are known. In most cases quantitative "resistance" is named what is observed as different incidence, falsified mainly by lateness and partly by R-gene effects. The former is important in long-day conditions.

First line a high part of additive gene actions as basic of general combining ability (GCA) were found in research on inheritance of quantitative foliage blight resistance (Tai & Hodgson 1975, Malcolmson & Killick 1980, Bradshaw et al. 1995b, Landeo et al. 1995, Landeo & Gastelo 1999, Haynes & Christ 1999). GCA dominated, but specific combining ability (SCA) was significant in a part of crosses (Bradshaw et al. 1995b, Haynes et al. 2007a). Over two years field assessment, broad-sense heritability was estimated of $h^2 = 0.79$ and narrow-sense heritability of $h^2 = 0.78$ on a diploid population of the *S. phureja* x *S. stenotomum* on AUDPC-data (Haynes & Christ 1999). From cycle two a broad-sense heritability was estimated of $h^2 = 0.71$ and narrow-sense heritability of $h^2 = 0.77$. These calculations assume half-sib structure of the 72 populations after open pollination, which is not sure and could be overestimated. The distribution of AUDPC groups underlined compatible host-pathogen relation in field assessment of this material. From two recurrent cycles a genetic gain was calculated, which the severity of foliage late blight will have been reduced by one-third (Haynes & Christ 2006), which is in the real level far from (below) breeders objective.

For population B at CIP $h^2 = 0.4$ -0.71 were estimated over four different locations (Landeo et al. 1995). Later $h^2 = 0.4$-0.53 was calculated (Landeo & Gastelo 1999, Landeo et al. 2000) and expected to be high enough to ensure further progress. Mendoza (1992) recorded medium to low heritability for horizontal foliage blight resistance. Gamboa et al. (2002) calculated $h^2 = 0.81$ for foliage blight in a diploid wild population using AUDPC; three QTL explained 55% of the variation which probably was not free from R-gene effects. Visker et al. (2004) found broad-sense heritability for foliage blight incidence of $h^2 = 0.49$-0.80 and for adjusted blight (regression to maturity) $h^2 = 0.39$-0.64, which should really describe late blight resistance. Broad-sense heritability of 0.39, 0.63, 0.55 and 0.93 are calculated by Bradshaw et al. (1999), of 0.57-0.75 by Yashina (1976) based on laboratory test. In *S. hougasii*-derived material Inglish et al. (2007) found a broad-sense heritability for rAUDPC from field of $h^2 = 0.83$; R-gene effects were not ex-

cluded. In seedlings progeny test parental scores and their GCAs correlated r = 0.87 (Bradshaw et al. 1995b).

However, non-additive gene actions (SCA) were ascertained to be more important for expression of field resistance than additive actions by Killick and Malcolmson (1973), Joseph et al. (1999) and Kaushik et al. (2000). High SCA effects could be realized regardless of parents GCA values (Joseph et al. 1999). A method to calculate GCA and SCA effects in pre-selected breeding populations is described by Haynes et al. (2007a); it does determine if GCA or SCA are significant and for which parents or combinations that is true. Parental phenotypes can be used as a first screen to select blight-resistant parents for use in a breeding programme (Bradshaw et al. 1995b). Gebhardt (1999) stated that QTL alleles which increase susceptibility to late blight often are dominant over alleles that increase resistance.

Since wild species mainly are sources of the used resistance and deviating ploidy level and/or differences in the genome structure are common irregular meiotic divisions followed by distorted segregation are often observed and complicate interpretation of inheritance and breeding planning (Salaman 1928, Rudorf & Schaper 1951, Swaminathan & Howard 1953, Hawkes 1990).

Some studies are conducted with dihaploid cross parents and compared with its tetraploid sources; by that mainly misinterpretations were produced. Contrary to all expectations van Suchtelen (1965) obtained frequently highly resistant dihaploids according to field observations – a result of retarded plant development and different microclimate. De Main (1978) assumed new genetic explanations for occurrence of superior dihaploids instead of thinking on ontogenic and environmental influences (habit, microclimate). Gorea et al. (1981) supposed cytoplasmatic inheritance of quantitative blight resistance. Parts of the inducer *S. phureja* are present in the genome of dihaploids and DNA rearrangement is demonstrated in dihaploid production (Ercolano et al. 2002).

Different expression of different polygenes in different stages of host development is assumed (Thoday & Thompson 1976, Tepper & Anderson 1984, Willmitzer 1987, Umaerus & Umaerus 1994, Gamboa et al. 2002), which could partly explain the quantitative cultivar-isolate interaction. However, different courses of resistance behaviour in different cultivars are also possible, if the compared clones possess different development (maturity) stages and the same genes for resistance (Lindqvist-Kreuze et al. (2010). The cultivar-isolate interaction is excluded by van der Plank (1963, 1969) for horizontal resistance, but was found by several authors on foliage or tubers (Jeffrey et al. 1962, Ullrich 1966, Caten 1974, Darsow & Meinl 1981b, Corbière et al. 2002, Miller et al. 1998, Flier et al. 2003a).

Results of research up to now do not require for marker-assisted selection (MAS) of quantitative blight resistance in breeding in general, only for special populations in some cases. However, discussed results give hope for development to this aim (Visser et al. 2009, Gebhardt et al. 2010). MAS is conceivable, if at minimum 70% of the genetic variance are explained by the markers used. In this way blight resistance could get a high priority in selection and the decision would be possible on seedlings or in the following year without any testing with the pathogen. However, that level is not reached in known studies. Depending from the year up to 50% of the foliage blight incidence (rAUDPC) could be explained by Marhadour et al. (2010) with three markers, however excluding of R-gene effects seems not sure. Wickramasinghe et al. (2009) could explain 23.4% of the total phenotypic variation of late blight incidence (AUDPC) in a diploid population by one marker. Simulation of MAS in a diploid population, in which the QTL were analysed, showed that 4 of 12 clones with the right alleles of markers were not resistant enough; outside of it 33 clones of 156 had not the optimal combination of QTL alleles (would be lost by MAS) but a good level of resistance (Sliwka et al. 2005). Problems of diagnostic potential of marker loci for MAS are explained by its species specifity or by recombination

events between marker locus and the resistance gene (Oberhagemann et al. 1999, Tan et al. 2005). Young (1999) recommended for QTL analysis at least 500 individuals per population and very accurate phenotyping. Next steps to make the mapping data ready for MAS are: repetition over several years and locations, testing in larger sibling populations and on genetically unrelated populations, use ore development of appropriate quantitative genetic analysis. After detecting and tagging enough resistance loci, the MAS will facilitate more efficient development of more resistant potato clones by selection of specified gene (QTL-) combinations, if universality of the molecular markers in a wide gene pool is given. The available results show that a long way for research is necessary.

2.7.2. Research on aspects of pathology of late blight resistance of both types

On the cellular level following can be summarized: Penetration of the pathogen into a leaf epidermis cell after inoculation with zoospores requires at least two hours, usually about four hours for development of an appressorium and additional two to six hours for penetration. Penetration of infection nail has mechanical and enzymatic activity (Pristou & Gallegly 1954, Shimony & Friend 1975, Sherwood & Vance 1982). Often the preinfectional processes did not differ between resistance types and resistance levels of the host, however several quantitative resistant clones need a longer 'inoculation access period' to establish an infection (Mueller 1931, Lapwood 1963, Umaerus 1970, Berggren et al. 1988). In incompatible host-pathogen interaction (hypersensitivity) cell death of penetrated potato cell can occur already about 9-12 hours after inoculation and the death of the pathogen about 12 additional hours later. In opposite, in a very susceptible cultivar after 48 hours penetrated cells are partly low affected (Mueller 1931, Shimony & Friend 1975) and the palisade and spongy mesophyll tissues are started to be extensively colonized. Berggren et al. (1988) stated the importance of early establishment of the hyphae in leaf tissue for the level of quantitative resistance. Resistant cultivars retarded hyphal growth from about 18-30 hours after inoculation on. However, Wilson & Coffey (1980) found high differences in frequency of penetration and growth rate of mycelium between cultivars of different level of quantitative foliage resistance; seeming hypersensitive-like reaction is possible without R-genes.

Some tuber-bearing wild species are found to be much higher resistant than cultivars (Thurston 1971), but none of them has shown immunity to *P. infestans*; in Central Mexico field conditions every potato species or selection has been observed to have at least a few late blight lesions from which the pathogen can be isolated (Niederhauser 1991). However, quantitative incidence with sparse sporulation is in itself insufficient proof of the absence of effective R-genes (Swiezynski et al. 2000b), because some R-genes do not complete suppress sporulation or its presence can exclude a part of inoculum from infection.

767 NB-LRR genes and gene homologues were identified in potato, which could be grouped in 10 known and 35 novel clusters (Bakker et al. 2010). Verweij et al. (2011b) mentioned 400 NB-LRR-genes which determine hypersensitive type of resistance. Some new R-genes were used in variable combinations by genetic engineering and selecting with high through-put technologies for major gene alleles of late blight resistance in seedlings stage with molecular markers in marker-assisted breeding (Carrasco et al. 2009). From R3a nine allelic versions are identified – additional chances and complications. Some homologous R-genes in different species are found, for instance *Rpi-blb1* is identified as homolog to *Rpi-sto1*, *Rpi-plt1, Rpi-pta1* and *Rpi-pta2*. *Rpi-sto1* and *Rpi-pta1* are functionally equivalent to *Rpi-blb1* (Hein et al. 2009). *R2*, *R2-like* and *Rpi-abpt* are found to be functionally equivalent to *Rpi-blb3* (Lokossou et al. 2009); *Rpi-phu1* is identical to *Rpi-vnt1.1* (Swiatek et al. 2011), which means that in different species the same or very similar major genes are expressed. Consequently, the available diversity of R-genes is smaller than expected. The hope of methodically more rapid and flexible diverse use of R-genes on cis-genic route compared with conventional breeding is the argument for going

back to renewed exploiting of a resistance type, being wrecked, in DuRPh project (Haverkort et al. 2009). Methodical progress in cloning and functional profiling of candidate avirulence genes is discussed by Vleeshouwers et al. (2010). However, understanding of effectors diversity in *P. infestans*, its expression and function is based on important assumptions (Birch et al. 2008, Slootweg et al. 2009). The gene RB (*Rpi-blb1*) is in *S. bulbocastanum* not expressed in tubers (Millett & Bradeen 2004). Regardless of that, durable resistance is contemplated (Haverkort et al. 2008); the term durable is here fictively used on an epidemiologically highly risky basis (Kuhl & Douches 2007). Even in Peru overcoming of *RB*- and *Rpi-blb2* resistance was found (Kreuze et al. 2011). In the Netherlands programme spatially and temporally separated deployment of different R-genes is intended (Kessel et al. 2010).

Carlisle et al. (2002) stated significant interaction between isolates and cultivars for quantitative overall resistance and all components assessed with 25 isolates and three cultivars on detached leaflets; no one isolate was the most aggressive across all three potato clones. Young et al. (2007) found a cultivar-specific effect on isolate distribution on foliage in the field, which was not correlated with isolate-specific aggressiveness on detached leaflets in North Ireland. It is concluded that additional factors other than aggressiveness mainly determine pathogenic fitness of isolates in the pathogen population in compatible host-pathogen relation, which are poorly understood.

Leaf position is more important than plant age and leaf age for detached leaf test in time of flowering (Visker 2005). However in seedlings test plant age is very important (Malcolmson 1980, Stewart et al. 1983c). In the final stage of vegetation foliage blight resistance has no survival value for the potato plant. Therefore is expected that the plant saves its effort in this stage and at the same time the chance of survival of the pathogen is increased (Mueller 1931, Robinson 1976).

2.7.3. QTL analyses on foliage blight resistance and its relation to maturity

Genetic loci, which contribute to the polygenic system of a quantitative trait, are termed QTL (quantitative trait loci). Molecular markers correspond to single genetic loci (QTL) and segregate in the progeny of parents differing in their alleles according to Mendelian rules. The molecular basis of all genetic markers is DNA mutations (Gebhardt 2007). Molecular markers are expected to improve the possibility, better to understand expression of quantitative blight resistance (Trognitz et al. 2000). Positional information on QTL and candidate genes for resistance may be used to identify and select superior alleles from cultivated and wild potato species (Gebhardt 1999). One or several QTL for quantitative foliage blight resistance were detected on all chromosomes of potato and for resistance of tubers on chromosome II, IV, V, VI, VII, VIII, IX and X (Meyer et al. 1998, Moreau et al. 1998, Collins et al. 1999, Oberhagemann et al. 1999, Ewing et al. 2000, Ghislain et al. 2001, Trognitz et al. 2002, Visker et al. 2003a, Bormann et al. 2004, Pajerowska et al. 2005, Bradshaw et al. 2004a, 2006b, Madsen et al. 2006, Sørensen et al. 2006, Simko et al. 2007, Trognitz et al. 2010, Marhadour et al. 2011, Truberg et al. 2011). No QTL was, however, detected consistently in several genetic backgrounds. This can be explained by the presence of different alleles at any given QTL in the genetic materials analysed. Segregation ratios at QTL for late blight resistance are often distorted, most with susceptibility alleles being more frequent than resistance alleles (Oberhagemann et al. 1999). Leonards-Schippers et al. (1994) identified the first race-specific QTL-locus for quantitative resistance. A candidate gene for quantitative late blight and *Erwinia*-resistance, which encodes a key enzyme in jasmonic acid biosynthesis, explained 12% of the late blight incidence (Pajerowska et al. 2005). Regions on chromosome III, IV and V are identified as hot spots for quantitative foliage blight resistance with high probability according to Simko et al. (2007). Because QTL for resistance are positioned on the molecular map with less precision than R-genes, it is problematic to compare the location of QTL from different studies (Simko et al. 2007). Most of these QTL were additionally associated with maturity

(Collins et al. 1999, Oberhagemann et al. 1999, Visker et al. 2003b, 2004); which reflects interpretation of "resistance" from disease severity without reduction of the maturity effect. Till today is discussed, whether plant maturity and quantitative foliage blight resistance are pleiotropic effects of the same gene(s) or are determined by physically tightly linked members of the same gene family (Gebhardt et al. 2004). This is a result of methodical incorrectness, using the level of attack (disease) as criterion of resistance, although disease severity results as mixed effect mainly from maturity. Such "resistance" is unavoidable obliged to overlap maturity.

Only few publications are known, in which a linear least-square regression was calculated of the **A**rea **U**nder **D**isease **P**rogress **C**urve of foliage blight (AUDPC) to maturity. Vertical distances of AUDPC or rAUDPC to linear regression line with maturity gave negative to positive values in an open scale and their average is always 0.0, the correlation to maturity is 0. These vertical distances are useful measure of true foliage-blight resistance (Darsow & Strahwald 2006, not published).

In this way Bormann et al. (2004) found one QTL for foliage blight resistance on chromosome II, III, V, VI, VII, VIII, IX, XII and two on chromosome XI. Seventeen marker alleles showed persistent effects in the same direction but of variable size in two or three years of testing, the average trait value over all years, or both. None of the marker alleles gave consistent results in both populations Escort x Leyla, Nikita x Leyla. The most persistent QTL-effects were associated with chromosome V, IX and XI_{ld} in both families and, in addition, on VIII, XI_{p} and XII in the Nikita family. Four to 12 % of the variance of resistance could be explained by a single maker allele in the first population, 4-17% in the second. Single interlocus interactions explained 9-24% of the phenotypic variance. Multiple regression analysis with forward selection showed that the effect of four QTL on chromosome V_{p}, $VIII_{ld}$, XI_{p} and XII_{ld} together explained 38% of phenotypic variance of resistance in the Nikita population, one QTL on chromosome V_{p} and XI_{ld} each explained 15% of phenotypic variance of resistance in the Escort population. It was calculated that the positive alleles of the best four QTL of Nikita family could be expected on 8 of 10,000 plants. The marker GP179-570 was in one population associated with resistance, in the other with susceptibility. Bormann et al. (2004) discussed that in diploid populations so far no more than 15 QTL for foliage blight resistance were detected and assume that 30 QTL may segregate in a tetraploid population.

Bradshaw et al. (2004a) examined a tetraploid full-sib family of 227 clones with 585 informative markers. One duplex QTL-allele on chromosome IV explained 31% of the variation for foliage blight resistance and 14% of tuber blight resistance on an additive model or 37% in case of partial dominance. A simplex QTL allele on chromosome V explained 18% of foliage blight variation and 26% of tuber blight variation, but when the residuals from the regression on maturity were analysed, there was no significant effect of a QTL on chromosome V. This statement shows the difference between the results in past, characterised as faulty development, and the correct procedure of calculation of foliage blight resistance. The major gene R7 had none significant effect on (maturity-corrected) resistance. Bradshaw et al. (2004a, b) discussed methodical limitations. Multivalents and double reduction, lack of complete homology between chromosomes, departures from random pairing, distorted segregation due to differential fertility and viability, errors in scoring gels, and genuine anomalies that require cytological explanation are not considered in the simple genetic model of interpretation. There is the question of whether or not a more elaborate and sophisticated theory is required for interpretation of molecular genetic results of quantitative traits for complex polysomic inheritance.

In publications of both groups the segregating populations were not optimal. Different results are given concerning the effect of a QTL on chromosome V to blight resistance and maturity. Whilst Bormann et al. (2004) assumed a pleiotropic effect on both, Bradshaw et al. (2004a, b) interpreted only a direct effect on maturity and an indirect effect by maturity on blight infestation. A QTL on chromosome IV was not associated with maturity and explained 24% of variation

in incidence of foliage and 24% in that of tubers (Bradshaw et al. 2004b). Two copies of the allele on chromosome IV gave higher resistance level than one copy. One QTL on chromosome V explained 55% of maturity variation of the progeny (Bradshaw et al. 2004a).

Special studies about association between late blight resistance and foliage maturity were presented by Visker (2005). Six dihaploid populations were assessed for relative AUDPC of foliage blight (3 x 2 plants in the field) and maturity type (3 x 3 plants, biweekly assessment between the beginning of August and mid-October used to calculate a rAUDPC too). An additional analysis was performed in which rAUDPC values for foliage blight were adjusted for rAUDPC of maturity type (Visker et al. 2004, Visker 2005). Three of the four used cross parents had very similar values as well for blight rAUDPC (0.60-0.65) as for maturity rAUDPC (score 4.2-4.6); the fourth was extremely late (1.8) with blight rAUDPC 0.54, all that far from being suitable plant material for such research. Maturity and blight incidence correlated r = 0.47-0.73. Adjustment of foliage blight rAUDPC (not enough understandable explained) indicated that there is genetic variation for late blight resistance on chromosome III and X that is independent from maturity. Another QTL was detected on chromosome VII only when blight attack was adjusted to maturity. However, the authors did not decide, only this independent part to recognize as late blight resistance from the mixed trait blight incidence. It is shown that assessment of maturity outside of breeding practice gives results inspiring little confidence in. Mainly results of one-year assessment in the field were analysed. Broad-sense heritability for blight incidence (h^2 = 0.49-0.80), foliage maturity (h^2 = 0.44-0.70) and adjusted blight (h^2 = 0.39-0.64) were calculated; the latter "was high enough to expect a reasonable response to selection" (Visker et al. 2004). GCA dominated in all three traits; SCA occurred also. Transgressions in both directions were found in blight rAUDPC and in maturity rAUDPC. In progeny 2 one QTL on chromosome VII accounted for 16% of adjusted blight rAUDPC, in progeny 5 two QTLs on chromosome III and X accounted for 17% or 12% each. Adjusted blight rAUDPC was confirmed only in two of the four used cross parents. In an additional dihaploid cross C x E a main QTL on chromosome V and one on chromosome III were localized, accounting for 41% and 25% of the variance of blight rAUDPC, respectively, whilst a significant interaction between both QTL's accounted for another 15% (Visker et al. (2003b). Only one QTL for maturity on chromosome V explained 84% of the total variance of the progeny. In case of blight rAUDPC data analysis with maturity as covariate the QTL on chromosome V for blight had about half of that found in the analysis of blight rAUDPC alone. Could this result be a hint on inadequate method of maturity assessment? The QTL for blight rAUDPC could not be distinguished from the QTL for maturity. Therefore, in that location one gene was assumed with pleiotropic effect on both or the presence of two closely linked QTLs, one pleiotropically regulating maturity and resistance, and another with an effect on resistance only. The discussion in Visker et al. (2003b) more than necessary underlined the old view: "The results also explain the virtual non-existence of potato varieties that are both early maturing and resistant against *P. infestans*", which is one ground of decision for the resistance concept realizing in the Netherlands Initiative on Late Blight 2003-2012 with the DuRPH project (Haverkort et al. 2009).

Bradshaw (2009) recognizes four types of field resistance :

1. one type associated with late maturity,

2. one type small in effect and associated with defeated R-genes,

3. QTL with large effect and *P. infestans* isolate-specific interaction,

4. a type still effective without resistance x isolate interactions and without large effect.

That is a summary on the today methodically dominating state of assessment of foliage blight resistance which is not able to separate qualitative and quantitative resistance because of low-input of scientific and practical possibilities for economical reasons. So, any correction of earlier "successes" as errors are avoided, and perhaps unintentionally, apparently scientific arguments are collected to turn away from quantitative type of resistance.

2.7.4. Relation of both types of late blight resistance

Confusion concerning the both types of resistance arose from several results of mainly last two decades:

1. Some QTL for blight resistance clustered near R-gene locations, for instance within a resistance hotspot on chromosome V (R1 and a QTL) and led to the speculation to be allelic forms of each other (Gebhardt 1994, 1999, Gebhardt et al. 2004). This speculation agreed with Nelson (1978) and Sidhu (1980), assuming a dialectic major or minor effect from the same genes, depending from the circumstances.

2. Genes of *S. bulbocastanum* were cloned and expressed in a susceptible potato, which became highly resistant against all races of *P. infestans* tested so far (Van der Vossen et al. 2005, Song et al. 2003). These preliminary results encourage the much easier use of qualitative late blight resistance in breeding and science; they push gene technique because of methodical advantages in science and breeding. Economic aspects of competition on the global potato market play a role in decisions how to go on (see chapter 10.3.).

3. In quantitative resistant potato clones hypersensitive reaction takes part too on a part of infection sites, it occurs somewhat later, less frequently and allows the pathogen to escape (Platanova et al. 1987, Vleeshouwers 2000, Vleeshouwers et al. 2000b). Similar effects seem to be known in other host-pathogen relations too (Heath 1976).

4. The incompatible reaction can be changed to a compatible one by narcotics (Mueller & Behr 1949) and *vica versa* by temperature (Mueller & Griesinger 1942, Mueller 1950b, Tomiyama 1982).

5. An isolate-specific QTL for quantitative late blight resistance in diploid clones was found (Leonards-Schippers et al. 1994).

6. Residual effects of R-genes or ghost-resistance of potato cultivars with overcoming R-gene resistance due to increased virulence of the pathogen population (van der Plank 1957) are mentioned as an open question since longer time. Several factors may take part in it, which has been to subdivide for resistance breeding. Some R-genes contribute to resistance by acting against a part of the local pathotypes of P. *infestans* by a filter effect, resulting in apparently quantitative resistance with delay of disease. Such inoculum could additionally cause pre-immunity (Mueller & Boerger 1941). It seems rather unlikely that direct interactions of defeated R-genes with minor genes on chromosomal level cause residual effects (Gees & Hohl 1988). However, combining of several R-genes in a potato clone may undesired has been introduced additional minor genes for quantitative resistance which cause the better quantitative resistance level (Mueller & Black 1952, Parlevliet 1983b, Wolfe 1993) than genotypes without or with lesser R-genes as is found by many authors (Toxopeus 1956a, Schick et al. 1958b, Lapwood & McKee 1961, Ullrich 1964, Zadina 1964b, 1965, Jeschke 1967, Konyayeva & Kiselyov 1975, Piotrowski 1975, Darsow et al. 1987, Swiezynski 1990, Stewart & Bradshaw 2001a). Own result is summarised in table 5. Assessment with compatible inoculum for the whole test material excludes other explanations in our experiment. The residual level can be estimated by testing with exclusively compatible inoculum instead of speculation after assessment with only partly compatible inoculum.

Table 5 Influence of number of R-genes in foliage on quantitative resistance (score 1-9) on tubers to *P. infestans* of potato cultivars and breeding clones, tested in compatible host-pathogen relation at Gross Luesewitz (Darsow et al. 1987). *: significant different to r, **: significant different to one R-gene at α = 0.05.

Number of R-genes	Number of clones	Mean value	Range of variation
Without (r)	458	4.0	1.8-7.3
One R-gene	227	4.8*	2.0-8.4
Two R-genes	165	5.0*	2.1-8.3
Three R-genes	16	5.2**	3.7-7.8
Four R-genes	16	5.2**	3.8-6.5

2.7.5. Induced foliage blight resistance

Some research is done to use induced resistance for protection against late blight (Doke et al. 1987, Stroemberg & Brishammar 1993, Cohen & Gisi 1994, van Loon 1997). Induced resistance resulted from combined action of several successive defence reactions (Stroemberg & Brishammar 1993) and was found most intensively on cultivars with highest quantitative resistance (Stroemberg 1995). Bengtson et al. (2011) propose to combine reduced fungicide application on cultivars of improved quantitative resistance with potato treatment using DL-beta-aminobutric acid (BABA). BABA activates the defence through the jasmonic acid pathway against necrophytes and through the salicylic acid pathway in case of biotrophic pathogens. For practical solutions multidisciplinary coordinated research is needed (Lyon & Newton 1997). This unspecific principle is difficult to handle and alone not enough effectively.

A new control strategy for *P. infestans* and some other pathogens of potato is expected by application of phosphorus acid on plants, which promotes resistance by inducing several defence pathways and by direct inhibition of the pathogens life cycle (Wang-Pruski et al. 2011).

2.8. State of breeding research for quantitative late blight resistance of tubers

2.8.1. Special complications concerning resistance of tubers

Remarks about resistance to late blight very often are directed exclusively to resistance of potato foliage against *P. infestans*. Generally the higher interest is focussed on foliage blight since more than 150 years (Mueller 1925, Vowinckel 1926, Lehmann 1938a). That is understandable for the 19th century and for the first period of use of hypersensitivity on foliage, in which the hope existed that spore production is nearly excluded to infect tubers. However, to consider both difficult polygenic parts of the dual disease resistance to late blight, that is a tremendous task for cultivar breeding. Moreover, methods for large scale-assessment in breeding practice are under discussion, even still today. According to Zimnoch-Guzowska & Flis (2002) tuber blight resistance was assessed only by 15 breeding enterprises and four institutes of 25 mainly European countries at that time; present-day the same is expected. Late blight resistance is named a multi-component-phenomenon (Clark 1978); that is true first line of tuber blight. Both, from an economical and from an epidemiological point of view, a high degree of resistance in tubers must be considered very important in moderate climate (Stevenson & Akeley 1953, Grainger 1957, Cox & Large 1960, Hirst & Stedman 1962, Mastenbroek 1964, Zadina 1964a, Mooi 1970, Nærstad 2002) and more important in quantitatively foliage blight resistant

cultivars (Stevenson & Akeley 1953, Frandsen 1958). Late blight resistance of tubers reduces primary inoculum density on foliage, reduces losses ascribed several other tuber rots during storage. However, its importance in other climatic and socio-economic conditions seems to be lesser (Forbes et al. 1998). Howard (1982, 631) wrote: "Although differences in resistance of tubers to infection by blight exists (Cox & Large 1960), breeding for such resistance has been on the whole neglected by breeders." This statement was true for the western part of Europe and for North America, but was lesser correct for Eastern Europe. Schick and Hopfe (1962) wrote that besides the foliage blight the tuber blight has an equal importance due to loss in storage primarily caused by *P. infestans*, undiminished on quantitatively foliage blight resistant varieties too. The big gap between necessity and real activity in breeding for tuber resistance continues up to now (Rogozina et al. 2001, Kirk et al. 2010). Additionally, increased pathogenicity of current populations mainly on tubers is described (Peters et al. 1999, Flier 2001). However, reliable assessment of tuber blight resistance is more difficult than foliage blight resistance. Increased interest on reliable tuber blight resistance of grown varieties exists for management of late blight control as factor in decision support systems last years.

Resistance mechanisms apparently differ for foliage and tuber blight, its quantitative resistances correlate low (de Bary 1876, Loehnis 1923, Vowinckel 1926, Lehmann 1938a, Schaper 1949, de Bruyn 1951, Stevenson & Akeley 1953, Wastie 1991, Flier 2001, Simko et al. 2007, Table 6). That requires handling both as independent traits in assessing and breeding (Holden 1977, Darsow 2000a). However, clones resistant on tubers often are resistant on foliage, but clones selected for foliage blight resistance may express susceptible to resistant tubers (Bhatia 1981, Glendinning 1989, Rahkonen et al. 2006). Table 3 illustrates its independence. Some authors think selection for tuber resistance in the first step of selection system lesser risky than beginning with selection for foliage blight resistance (Montaldo & Akeley 1946, Sieczka et al. 1992) concerning the type of resistance.

Quantitative foliage and tuber resistance are mainly controlled by different genes (Stevenson & Akeley 1953, Stewart et al. 1992, Flier et al. 1998, Oberhagemann et al. 1999, Flier 2001, Haynes & Christ 2006, Simko et al. 2006, Liu & Halterman 2009). On molecular genetic level lesser information is available about the genes affecting resistance in tubers compared to foliage (Simko et al. 2007). One or several QTL for quantitative tuber blight resistance were detected on chromosomes II, IV, V, VI, VIII, IX and X (Collins et al. 1999, Oberhagemann et al. 1999, Ghislain et al. 2001, Bradshaw et al. 2004a, 2006b, Simko et al. 2006, 2007). Mechanisms of resistance to penetration and resistance to spread in tuber tissue are largely unexplained (Friend 1991, Parker et al. 1991, Flier 2001), its inheritance too (Wastie 1991, Swiezynski & Zimnoch-Guzowska 2001). Toxopeus (1961) selected most quantitatively resistant clones from progeny of two resistant parents, but from crosses susceptible x susceptible also some. Ratuszniak (1981/82) calculated heritability for tuber blight resistance in slice test $h^2 = 0.13$. In a diallel of 10 cross parents general combining ability (GCA) and specific combining ability (SCA) were significant for tuber blight as well as the interactions of both with the years of assessment. Bradshaw et al. (1999) calculated broad-sense heritability of $h^2 = 0.76$-091 in single-year assessment of whole tubers from progeny grown in greenhouse. In seedlings progeny test parental scores correlated with their GCAs $r = 0.76$ in tuber blight resistance (Bradshaw et al. 1995b). Quantitative pathogenicity (aggressiveness) of *P. infestans* isolates can differ for foliage and tubers (Flier et al. 2003a) and its increase mainly for tubers is stated (Peters et al. 1999).

Tuber blight attack in the field is substantially influenced by intensity of spore production of *P. infestans* on the foliage of a variety (determined 38%, Darsow & Oertel 1986), by the amount of precipitation and its distribution in time during period of foliage blight (Cox & Large 1960, Lapwood 1977, Karaseyeva 1979). Other factors are the type of soil, placement of tubers in the hill, length of stolons or tuber distance to the main stems (Lacey 1966) and resistance of tubers. The resistance determined only 14% of the result according to tuber slice test (Darsow & Oertel

1986). Cultivars with high susceptible foliage may remain free of tuber blight; and resistant foliage prolongs potentially duration of sparse sporulation on foliage and increases the probability of tuber infections by washing down of spores (Boyd & Henderson 1953, Toxopeus 1958, Takase & Umemura 1966). Therefore naturally tuber infections in the field by spores produced on the foliage are not suitable as criterion of tuber blight resistance and not a criterion of reliability of a test method for tuber blight resistance. Special methods of assessment of resistance are necessary (see chapter 4.3). Repeated low to middle correlation of such methods were found to infection in the field via foliage of r = 0.53-0.59 (Darsow 1983a, Flier et al. 2003a, table 6). In tuber blight resistance two components are important: resistance to infection (to establish the pathogen) and resistance to spread of mycelium in tuber tissue, visible as browning or aerial mycelium. Research on tuber-resistance mainly has been carried out on resistance to spread of *P. infestans* in tuber tissue, and the most applied methods of assessing resistance of tubers inoculate tuber medulla or damaged cortex. However, resistance to infection and resistance to spread (test of whole tubers compared to slice test) did not correlate (r = 0.05-0.2, Darsow 1983a).

Tuber resistance tends to be much lower correlated to maturity than foliage blight resistance according to own experience and most other researchers (Toxopeus 1958, Moo 1970, Swiezynski 1990, Swiezynski & Zimnoch-Guzowska 2001). However, Swiezynski et al. (1993) concluded that a high level of tuber resistance is difficult to combine with early maturity. A tendency of increased susceptibility in late to very late clones in slice test could be explained by different state at harvest or co-evolutionary adjustment for surviving of the pathogen (Darsow 1983a).

2.8.2. Resistance to infection

Quantitative resistance to *P. infestans* continuously changes during tuber development, growing, maturing and tuber storage. Considering the known results of tuber infections, so a dynamic, ontogenic predisposed development seems to occur from very young highly resistant tubers (Loehnis 1922, Darsow & Meinl 1981a) to maximal susceptibility before maturing, about in first half of August (in Europe) depending from maturity group, followed by increased resistance towards harvest of mature tubers (Loehnis 1925, Bonde et al. 1940, Boyd & Henderson 1953, Zan 1962, Lacey 1967a, Lapwood 1967, Walmsley-Woodward 1974, Malcolmson 1980, Stewart et al. 1983b, Kadish et al. 1991, Grinberger et al. 1995, Darsow 2004/05 b). This tendency in resistance to infection may widely vary due to abiotic and biotic factors, but mainly by soil moisture. Over that, different sites of entrance differentially take part in this tendency (Zeck 1957, Lapwood 1961c, Walmsley-Woodward & Lewis 1977, Darsow 2004/05 b).

Tuber infections occur especially easy on deep wounds. Other sites of entry are eyes, lenticels, the hilum, growth cracks and spots of powdery scab (Mueller 1931, Schultz 1952, Lapwood 1961a, 1977, Lacey 1966, 1967a, Ullrich 1967, Walmsley-Woodward & Lewis 1977) with cultivar-specific preference (Lapwood 1961a, Davila 1964, Darsow et al. 2004/05 b). 200 lenticels and 10 eyes are counted in average on a King Edward tuber which covers about 5% and 1% of the tuber surface (Lacey 1967a, Lapwood 1967). Entrance via lenticels leads the pathogen into phelloderm and cortex with general higher defence potential (Loehnis 1923, Toxopeus 1958, 1961, Lapwood 1965, Fehrmann & Dimond 1967, Noll 1968, Cupsa 1974, Adams 1975); vascular bundle constitutes a barrier. Figure 4 shows lenticel infections on a quantitatively resistant clone about eight days after inoculation. Cultivars differ in its number and size of lenticels per tuber and react differently on ambient soil moisture (Meinl 1966). Proliferated lenticels result from temporary (>6 days) high soil moisture; they attract zoospores more intensively and facilitate entry of the pathogen (Walmsley-Woodward et al. 1975); tubers become more susceptible (Loehnis 1923, Vowinckel 1926, Lacey 1967a, Adams 1975, Darsow 2004/05b). High soil moisture, especially in clay soil, resulted in lenticels filled with unsuberized parenchyma cells, which easily can be attacked. Darsow and Meinl (1981a) showed under controlled soil moisture with

50% and 100% water holding capacity of soil in average of three cultivars 87% of total tuber infections via lenticels. Lenticels become less susceptible as the tuber matures (Loehnis 1925, Bonde et al. 1940, Zan 1962, Lacey 1967a, Walmsley-Woodward et al. 1975, Darsow 2004/05b). They remain closed in good storage conditions. Reduced entrance through lenticels may be explained by its suberization as tubers mature and are stored; formation of cork cambium differs in years (Lacey 1967a) and with fluctuating soil moisture (Darsow 2004/05b). Periderm thickness was greater in wet soils compared with the dry ones and increased cultivar-specifically with tuber age. However, there was no clear relationship between the degree of suberization of lenticels during tuber development and their frequency of penetration (Tyner et al. 1997).

The eye is more complex than the lenticel and is not uniformly susceptible at all over; four sites of eye infection are differentiated with following part of 1358 infections records: 1. the scale leaf on the brow (32.7%), 2. lenticels on brow of the eye (7%), 3. the central bud in the axil of scale leaf (40.8%), 4. the usual two lateral buds (19.5%, Lacey 1967a). Walmsley-Woodward & Lewis (1977) stated a tendency of reduced susceptibilities of eyes towards the harvest, but with high variation, significant differences between years, however not between cultivars; the opposite found Loehnis (1925). Before harvest eyes are most frequently infected (Hecke 1898, Vowinckel 1926, Lapwood 1961a, Lacey 1967a). Entrance of *P. infestans* through eyes increased from 55-100% in August to 90-100% in February after storage (Zan 1962). In own research 50% of total infections occurred through lenticels and 35% through eyes (average of three years); tubers of 41 cultivars were inoculated by dipping in suspension one day after harvest. Eye infections were the most important ones and showed the most significant cultivar differences compared with other sites of entrance in average of cultivars, years, methods and all its interactions. They usually caused rotting of tubers in opposite to entrance via lenticels. In our routine test method eye infections correlated best with the overall tuber resistance ($r = 0.6$). The five most resistant cultivars comparing with the five most susceptible ones showed 36% lesser entry of the pathogen via eyes and similar part through lenticels (Darsow 2004/05 b). Tuber infection through an eye is shown in figure 5 about seven days after inoculation.

The junction between stolon and tuber plays in some cultivars a role (43% in Sieglinde), in general about 12% of total infections occurred through the hilum in average of 41 cultivars and three years (Darsow 2004/05b). However Walmsley-Woodward (1974) considered the hilum as important site of entrance. Stewart et al. (1983a) ignore infections via hilum in assessment of tuber resistance. Infection via hilum is connected with quick progress of disease (fig. 6).

Thread-like lesions occur on some clones under determined conditions on the outer cortex. These unusually flat lesions may harbour the pathogen latent, it rarely appears to be re-activated (Wastie 1991).

According to Zadina (1950) the resistance of tubers correlated with thickness of skin; that could be explained by relation between susceptibility to damage and frequency of infection. Superficial wounds partly do not allow the pathogen to spread into deeper layers of tuber tissue (Darsow & Meinl 1981a). Growth cracks played a role in some years in some cultivars (Lapwood 1977).

Considering the evolution of the host-pathogen relation, eye infections may be the preferred entrance of the pathogen under adverse conditions to establish the disease. Entrance *via* eyes makes frequently colonisation because of having a way of spread nearly without barriers, but the high risk of rotting. The main part of lenticel infections caused arrested lesions. In comparison to eyes entering *via* lenticels seems to be a stable way to co-exists in suitable environmental conditions, but with lower probability of spread of the mycelium and the lowest risk of tuber rotting, because of the often higher defence reaction of the periderm and the barrier of vascular ring (fig. 7). Probably it is the most efficient entrance for owerwintering in seed potatoes as source of primary infections next vegetation. This view is supported by the results of van der Zaag (1956) that a chance of an infected seed tuber to produce a primary focus of foliage blight

is the greatest at a distance of 3-4 cm between a hibernating lesion and the next healthy eye. During vegetation up to maturity of tubers ontogenic factors seem to regulate environmental influences on tuber blight resistance. High soil moisture in the beginning of August had much lower effect than in September.

Remarkable cultivar-specific differences occur in the proportion of entrance *via* eyes, lenticels, wounds and the hilum (Bonde et al. 1940, Montaldo & Akeley 1946, Lapwood 1961b, 1977, Walmsley-Woodward & Lewis 1977, Darsow 2004/05b). In general entrance *via* lenticels was in inverse ratio to eyes, because entrance *via* wounds or hilum played a subordinated role in using of gentle harvest technique. According to Lapwood (1977) the relation of infections via eyes and lenticels varied with the year. Clone-specific reactions were stated on increased soil moisture, on time of harvest, on density of inoculum, on intermediate storage (Darsow 2004/05a, b, Lebecka et al. 2006). Also duration of the period of most resistant level of each clone (variety) during storage differs from each other and seems related to dormancy (Swiezynski et al. 2001). These interactions are crucial for the purpose, to find a reliable, simple and quick method of assessment of tuber blight resistance to infection for breeding. However, such existing interactions are characteristically for quantitative, polygenic resistance and has stepwise to be considered in the method for the most relevant range of environmental and agro-technical conditions in the region of intended growing of the potato cultivar (climate, type of soil, irrigation or not, progress of foliage blight, technique of harvest and in storage) by assessment as possible from 2-3 locations and for three years. Most important is the predisposition from the vegetation conditions in assessment of resistance, in which soil moisture and temperature play an important part. More difficult is, that on cultivar Cara in Ireland local adaptation of the pathogen population was obtained which resulted in higher aggressiveness on tubers (Dowley et al. 1991). Such rare events as partly adaptation by mutation can not be excluded, but underline considering of other measures of plant protection as crop rotation and diversity of cultivars. Flier et al. (2001) stated cultivar by isolate interactions for percentage of colonized tubers (cortical resistance) as well as for intensity of colonization of the tuber volume recorded on area after longitudinal cut (invasive ability index).

What is the basic of a reliable method to assess tuber resistance to entrance of the pathogen? Probably testing near the highest susceptibility at beginning of maturation is representative for disease course in the field, because infections in our potato production in Central Europe occur mainly before harvest (Stephan 1970) and partly during digging and transport (Dowley und O'Sullivan 1991). In such preconditions a test of whole tubers freshly after harvest without visible wounds should have the highest priority, if the used technique for harvest, transport and storage far-reaching avoids damage of tubers. Important is to inoculate within 24 hours after harvest to rule out effects such as skin and lenticel hardening (Stewart et al. 1983b). But there are problems in some details.

Local inoculation of field-grown King Edward on eyes or lenticels were compared with general spray-inoculation of tubers over three years, four to eight dates per year from July to September. The results show high variability from date to date and between the years. Local inoculation of freshly harvested tubers on eyes or lenticels resulted in 65% infections via eyes and 20% via lenticels, whereas spraying of tubers infected 990 lenticels and 368 eyes (Lacey 1967a). In wet soil young tubers were mainly (71%) found to be infected through eyes, whilst larger and elder tubers were preferred infected (84%) via lenticels (Darsow & Meinl 1981a). How to test in the best manner? Practical aspects of inoculation should decide.

Tuber blight resistance to infection is determined by morphological and physiological state of tubers at the moment of assessment (Stewart et al. 1983b, Darsow 1988a) or the mode of inoculation. Since the efficiency of points of entrance differs and changes with plant age and during storage, with environmental conditions and level of resistance (Boyd & Henderson 1953, Lacey 1967a, 1967b, Lapwood 1967, 1977, Walmsley-Woodward & Lewis 1977, Darsow & Meinl 1981a,

Darsow 1983a, 1988a, 2004/05a, b, Bhatia & Young, 1985, Grinberger et al. 1995, Kirk et al. 2001), the method could include standardization for maturity state at harvest and partly influence the soil moisture last 10 days before harvest.

Lower inoculum density is necessary to infect tubers compared with leaves. Fewer than 500 sporangia per ml found Lacey (1967b) on soil surface, 10% of tubers became blighted from inocula containing 100 sporangia per ml (Lacey 1967a); at least two sporangia per ml infected successfully (Fehrmann 1963). That agrees with the possibility of remarkable tuber infection from low foliage blight incidence (Toxopeus 1958, Lapwood 1971). Zoospore suspension in a range between 5,500 and 43 sporangia per ml inoculum density was found infective (Darsow 2004/05b). Diluting the spore suspension decreased the entrance via lenticels more than via eyes (Lacey 1967a), and via lenticels cultivar-specific more then through wounds (Davila 1964). However, a broad range of pre-breeding material showed that clonal-specific interaction of inoculum density with entrance via eyes or lenticels occurs. Even if two different soil moisture variants 10 days before harvest did not cause significant different tuber incidence, the interaction of clones with soil moisture was significant (Darsow 2004/05b).

The soil type influences susceptibility of tubers, more infections occur in clay than in sandy soil (Loehnis 1923, 1925). Van der Zaag (1956) found on cultivar Eigenheimer more tubers infected via lenticels from clay. Soil temperature is a factor influencing tuber blight infections; high temperatures are found the reason of very rarely tuber blight in South Japan (Sato 1979). Eye resistance of cultivars could better be differentiated at 10°C (Langton 1972). Changing of microbe relations on the surface of the potato tuber or in the tuber tissue influence the host/*P. infestans*-interaction (Lacey 1965, Adams & Lapwood 1978, Clulow et al. 1995) and are modified by environmental conditions as soil moisture (Lewis 1970, Adams & Lapwood 1978). Dry stress can increase the susceptibility of tubers for infection in following period (Stewart et al. 1993), which is to consider in growing in greenhouse and in the field.

In SCRI Dundee Stewart et al. (1994, 1996) found that the environmental component of variation in assessment of whole tubers in the field was greater than for foliage blight in the field. Interactions cultivar x year, cultivar x harvest date, and year x harvest date are often stated to be significant (Darsow 1983a, Stewart et al. 1996, Flier et al. 2001, Darsow 2004/5a). Tests of glasshouse-grown tubers were found more consistent over years than those done on field-grown tubers and stated partly sufficient correlations to test samples grown in the field (Stewart et al. 1996, see table 6). They decided in this manner partly to standardize the growing conditions too concerning soil, soil moisture and temperature (Stewart et al. 1993) and apply assessment of greenhouse-grown tubers only (Stewart & Solomon-Blackburn 2004). At ILK Gross Luesewitz and IHAR Mlochow field grown tubers are assessed (chapter 4.4.). It is not known if lesser representativety of greenhouse-grown tubers includes the higher error in selection than assessment of higher variable predisposed field-grown tubers.

2.8.3. Resistance to spread

Microscopic investigation on tuber tissue is carried out with tuber slices mainly. Cells of tuber pith are several times larger than of leaves with thicker walls. First differences between compatible and incompatible host-pathogen interaction could be observed 24 hours after inoculation with zoospores in the potato cells. Only little wall apposition was detected in penetrated cells. *P. infestans* seems to form longer a more stable biotrophic relationship with tuber cells than with leaf cells. Both, penetration and intercellular growth of mycelium involved changes in the host cell wall (Shimony & Friend 1976). Potato clonal differences in time between inoculation and development of aerial mycelium on the opposite surface of tuber slices is largely due to differences in the time required for the establishment of infection and not due to different growth rate (Clarke & Kassim 1977). The tissue surrounding a penetrated cell is involved in the defence reaction (Tomiyama et al. 1958). Detached immature potato tubers and stolons are more sus-

ceptible than inserted ones after wound inoculation (Darsow & Meinl 1981b).

Deeper wounds are dominating sites of entry of the pathogen during harvest and transport of tubers (Lacey 1967a, Darsow & Meinl 1981a). Therefore damaging of tubers has to be avoided by improved technology and by reduced tuber susceptibility to injury.

Most applied methods of assessing resistance of tubers have been carried out on resistance to spread of *P. infestans* in tuber tissue inoculating tuber medulla or damaged cortex. Late blight infection suppresses cell division and wound periderm development of potato tissue (Hamilton et al. 1980). Wounding of tuber tissue before inoculation means an additional factor of stress with mobilizing and competitive effect (Ishizaka & Tomiyama 1970, Sakai et al. 1979, Smith & Rubery 1981, Oba et al. 1982). Wound healing has priority over specific defence reaction (Lulai 2007) and is finished in the cortex quicker than in tuber pith; its course depends on physiological stage of tuber (maturity) and variety (McGee et al. 1981). One to five hours after cutting the level of resistance was reduced, maximal after 2-3 hours, whereas after 10 hours resistance level was significant enhanced (Furuchi et al. 1979, Darsow 1986). Wound infection in practice occurs partly simultaneously with wounding and is mainly finished 4-5 hours after wounding by harvester (Shimony & Friend 1977). Because of clone-by-wound healing interaction and reduced differentiability of pre-breeding material after extended wound healing before inoculation some authors applied the test without it (Darsow 1986). Other authors included wound healing in assessment of cultivars (Schoeber & Hoeppner 1972, Deahl et al. 1974, chapter 4.3.) because of better relation to tuber infections in the field (a dubious argument) and lesser problems with disturbing infections by *Erwinia* sp. and *Fusarium* sp. or improved differentiation of tuber blight resistance (Swiezynski & Zimnoch-Guzowska 2001).

The spread of *P. infestans* in tuber tissue and tuber infection through eyes or lenticels are found to be not correlated (Flier et al. 1998). It is concluded that these components of aggressiveness of the pathogen are controlled by different mechanisms (Flier et al. 1998). Flier et al. (2001) tested nine cultivars on whole tubers and slices and found disease severity in whole tubers very low correlated with necrotic area and mycelium density in tuber slice test ($r = 0.26$-33). The number of infected tubers correlated to its blighted tuber part in whole tubers with $r = 0.88$; infection frequency of whole tubers correlated to necrotic area and mycelium density on slices with $r = 0.16$ and 0.36. Both components of resistance in the slice test correlated with each other with $r = 0.46$. No correlation was found to the resistance level in the Netherlands variety list ($r = 0.09$-0.32).

An interaction year-by-cultivar is often described (Pietkiewicz & Jellis 1976, Darsow 1983a, Lebecka et al. 2006), year-by-isolate, year-by-location, pathotype-by-location, location-by-cultivar too (Darsow 1983a, Flier et al. 2001). A significant cultivar-by-isolate interaction, which account for about 10% of the explained variance of resistance, found Flier et al. (2003a) in whole tuber test and tuber slice test for all components studied. That confirmed earlier results in compatible pathogen-host relation (Jeffrey et al. 1962, Ullrich 1966, Caten 1974, Darsow & Meinl 1981b, Bjor & Muledid 1991) which hint to the possibility of adaptation with small steps of the pathogen population on principle. However, in research of Flier et al. (2001) compatibility of used isolates existed probably only for the main part of host-isolate combinations. The consequence is to assess with at least two aggressive and compatible isolates.

Most research on tuber resistance is done with wound inoculation of tuber tissue concerning growth of the pathogen mycelium. Most susceptible cultivars can be infected at ≥ 6°C, other only at ≥ 10°C (Ullrich 1977). Already Mueller and Griesinger (1942) showed that the temperature after inoculation influences speed of colonisation of tuber tissue and in different manner effects on browning and development of aerial mycelium; the temperature modifies the visible difference between cultivars of different level of resistance. The optimal range for assessment of resistance to spread is assumed between 16 and 21°C. Generally test temperature near 15°C is preferred, which resulted in a higher level of resistance because of lower spread of the

pathogen in tissue and at the same time higher density of aerial mycelium (Jeschke 1967) and requires longer duration of the monocyclic tests. Sometimes first hours after inoculation 10-15°C are applied followed by 18-20°C (Lacey 1967a, Lapwood 1965). In slice test of pre-breeding material with higher level of resistance stronger conditions has been preferred, 19°C enabled the best discrimination of clones (Darsow 1987a, b). Interactions of temperature-by-isolate and temperature-by-cultivar were significant (Thompson & Cooke 2005).

Growing of mycelium in tuber tissue can visually not directly exactly be observed, the pathogen has invaded more tissue than shows necrotic change or sporangiophores as sign of reproduction. Tissue colonisation may visually be estimated by area of browning or/and area with aerial mycelium. Additionally density of aerial mycelium is considered. Measuring in mm has principal no advantage to visual estimation in % or score (Darsow 1991a), but requires about five times more time. Vowinckel (1926), Mueller (1935) and Lapwood (1965) considered browning of tissue as less suitable to estimate tuber incidence as criterion of quantitative resistance because cultivars differ in intensity and course of time; additionally different parts of tuber tissue react differently, and pathogenic isolates may cause different expression of browning or aerial mycelium. Cultivar-specific reaction in relation of browning to aerial mycelium were stated by Haenni (1949) and Huettenbach (1951) and confirmed by own results. Therefore Oertel (1972) decided to consider only the worst expression of both on each slice, respectively, for clone evaluation. Therefore scanning of tuber tissue with a flatbed scanner to determine the average reflective index of browning as objective method (Douches et al. 2002b) is critically considered by us.

Different expression of resistance to spread in cortex and medulla of potato tuber was detected (Vowinckel 1926, Lapwood & McKee 1961, Lapwood, 1965, Førsund & Roer 1964, Jeschke 1967, Deahl et al. 1974, Durska 1975, Pathak & Clarke 1987, Oberhagemann et al. 1999). Therefore in some methods tubers are damaged only few mm deep (see 4.3.3.).

Spore density of suspension for inoculation is important; discrimination of clones tested declines outside of optimal density, depending from potato material, applied method, conditions in growing season, and physiological stage of potatoes at the moment of testing. An interaction pathotype or isolate x spore density and potato clone x spore density are described (Darsow & Meinl 1981a, Darsow 1987a).

The year of growing as sum of conditions during vegetation is a frequent source of variance in assessment of resistance to spread, but the interaction clone-by-year is a major one (Darsow 1987a, Flier et al. 2001, Lebecka et al. 2006). For comparison of potato clones in slice test the critical difference was smaller in three years average with two replications than in 12 years average without replication. Calculation of variance components gave a 1:3:28 ratio for the factors year, clone x year, and potato clone (Darsow 1987a). Some clones react more stable, other more intensively. Location of growing is a next important complex environmental factor which should be considered in testing of potential cultivars for resistance to spread too. According to own experience irrigation affects the resistance more than fertilization.

Harvest date, month of testing, and sprout stimulation significantly influence the result of slice test (Bhatia & Young 1985, Darsow 1988a) and of whole tubers including interaction with the potato genotype and year (Lebecka et al. 2006). It is not known which metabolic substances in the tuber determine the changing resistance (Henniger 1966). Highest resistance level occurs during autonomous dormancy; its beginning and end are clone-specific varied by complex factors of vegetation and storage. Therefore slice test is recommended after a waiting period to harvest of about three weeks and to finish before end of December (Huettenbach 1951, Barskaya et al. 1978, Bhatia & Young 1980, Chalenko et al. 1980, Darsow 1988a). Lebecka et al. (2006) found clone-specific change of resistance level between late July and end of February with most stable expression between middle of August and mid November. Tissue of small tubers at harvest is frequently more susceptible, partly cultivar-specifically (Jeschke 1967, Hen-

riksen 1969, Darsow 1987b), although tuber size is not a strong measure of physiological age (Raeuber & Engel 1963). Usually tubers of middle size are used. Tuber segment from which the disk was cut was of minor, but significant influence on resistance and showed cultivar-specific expression (Darsow 1987b). A significant interaction cultivar-test temperature was stated by Jeschke (1967). Storage temperature before testing is another factor for standardization in assessment of resistance (Fehrmann 1963). Short-term changing three days prior to testing from 22°C to 12°C increased the resistance more than the difference caused by successive storage on both temperatures in parallel for a month. Short-term cooling always resulted in enhanced resistance; warming from 12°C increased the resistance, and warming from 6°C reduced it (Darsow 1987b). Several authors pointed to deviating results of blight resistance because of virus infections of tested potatoes (chapter 2.4.). Virus diseases produced different effects, depending on cultivar, year, date of testing, inoculum density and virus species. The effect of the same virus infection differed frequently between foliage and tubers of the same cultivar depending from the year (Darsow & Wulfert 1989a, b, see 2.4.). These disturbing effects can be excluded by standardization.

2.8.4. Decision for a method or methods of tuber blight assessment

A lot of methods have been developed to assess tuber blight resistance (see chapter 4.3.). It is difficult or impossible to consider in a method all components of resistance and the main factors of influence. In addition, the best physiological state for assessment is not surely known. Due to wide range of maturity compromises are necessary. Testing tubers with wounding before inoculation are preferred by many authors because of three advantages: lesser tuber number is necessary; testing in winter is possible; better reproducibility of the results. Practical advantages substantiate dominating variants of tuber slice test.

However, the method should be selected according to biological aspects first line. For that, results of table 6 are discussed. Our standard method (net bag test) assesses undamaged whole tubers immediately after harvest. This test was compared with assessment of damaged whole tubers after about four month storage and test of tuber slices. The slice test is part of our testing system too. (Details are given in chapter 4.4.). The comparison of the methods showed the dominant effect of interaction years x methods and of methods (Darsow 2004/05 a). Next important source of variance was factor varieties. Additional the interactions varieties x years and varieties x methods were significant. Assessment of stored and wounded whole tubers showed 50% (23-76%) eye infections, 28% (13-49%) through wounds, 14% (5-33%) through lenticels, and 8% (0-19%) via hilum. Data in brackets mean the range of cultivar reaction. The five most resistant cultivars differed from the five most susceptible ones in assessment in August by 62% lesser entry through eyes, relatively more lenticel infections as small, arrested lesions from total detected sites of entrance and 21% lesser entrance through injuries (Darsow 2004/05b).

Table 6 Tuber blight resistance of 41 varieties, calculated over 3 years, 3 methods (bag test, test after storage, slice test). Table of variances (1: sums of squares; 2: degrees of freedom; 3: mean squares; 4: variance of ratios; 5: F-probabilities, *: significant effect), Darsow (2004/05a).

Sources of variation	SQ[1]	DF[2]	MQ[3]	$F_{exp.}$[4]	$F_{tab.}$[5]
Total	423.82	368	1.15	-	-
Varieties	94.41	40	2.36*	3.87	1.54
Methods	22.18	2	11.09*	18.18	3.05
Years	0.13	2	0.07	0.11	19.49
Varieties x years	71.12	80	0.89*	1.46	1.36
Varieties x methods	85.95	80	1.07*	1.76	1.36
Years x methods	52.45	4	13.11*	21.50	2.43
Rest	97.58	160	0.61	-	-

Each of these testing methods considers different components of resistance behaviour. A phytopathologist prefers reproducibility as main point of view for a method to assess resistance. A breeder has to deal with the practical consequences of the selection and has more to consider, which components of resistance probably have the highest effect under present and future growing conditions. That is the conflict between reproducibility and representativety. Methods with wounding of tubers are suitable for potato production with a lot of severe injuries of tubers and for varieties with high susceptibility to tuber damage. The early strategy at Gross Luesewitz was based on tuber slice test without wound healing because of damaging harvest machines (Darsow 1987a) at that time. That time a complex programme in pre-breeding for late blight resistance was conducted by combining tuber blight resistance with resistance to tuber damage on the one hand and resistance to *Erwinia carotovora* ssp. *atroseptica* and *Fusarium* sp. on the other hand (Darsow and Roeber 1998, Darsow 1998b, 2000a). Rapidity of periderm formation is an additional trait, which could be considered in this complex of factors to reduce wound infections.

However, resistance to entrance of the pathogen is more difficult but more appropriate in considering the whole range of defence mechanisms. Probably a first selection step on young breeding material on immature greenhouse-grown tubers according to Stewart & Solomon-Blackburn (2004) can be recommended for negative selection. A three-year assessment of field-grown tubers spray-inoculated (Stewart et al. 1983b) or by dipping in suspension (Darsow 1983a) should be applied for last step of selection of cross parents and cultivar candidates based on several years' average. Near the period of ontogenically determined highest tuber susceptibility (in mid-August) seems the best date of whole tubers test (Lacey 1967a, Stewart et al. 1983b, Darsow 1983a). Washing of tubers before inoculation makes easier to see the symptoms, but influences the level of infection (Clulow et al. 1995, Lozoya-Saldana & Caballero 2000). According to Lapwood (1967) the part of weight of invaded tuber tissue is the best measure of resistance. Enough personal experience enables visual estimation.

Some correlations between foliage blight and tuber blight, different methods or different years of testing are shown in table 7. Largely short information is given about conditions of cultivation, for instance grown in greenhouse or field and which method was used. Because tested material plays a role for the result, partly remarks are given as 11 populations (pop.) or diverse (div.) more wild material, cultivars with R-genes, cultivars with *S. demissum* in its parentage (*dms*). Not publish. means not published. A range of correlation coefficients stands for the range of different populations or different material groups. Deahl et al. (1974) established that

the evaluation method may influence the correlation. Erjefaelt (1975) found resistance of tuber tissue (slice test) only correlated with resistance to spread in single leaf test. The mainly low to middle coefficients in table 7 underline

1. the necessity to select for quantitative foliage and tuber resistance independently,
2. relative independence of components of resistance,
3. high environmental influence.

More research on tuber blight has to support the right manner of assessment in breeding.

Table 7 Correlations with late blight resistance of tubers

Traits, methods, conditions compared		r	Reference
Foliage blight resistance	: Tuber blight resistance	0.54-0.57	Mueller 1949
Foliage blight resistance	: Tuber blight resistance	0.45	Piotrowski et al. 1973
Foliage blight resistance	: Slices freshly inoculated	0.44	Deahl et al. 1974
Foliage blight resistance	: Slices after wound healing	0.87	Deahl et al. 1974
Foliage blight resistance	: Tuber blight resistance	0.01-0.32	Yashina et al. 1974
Foliage blight resistance	: Tuber blight resistance	0.06-0.73	Pietkiewicz 1976
Foliage blight resistance	: Tuber blight resistance	0.346	Anonymous 1985
Foliage blight resistance field	: Tuber slice test field-grown	0.35-0.58	Darsow 1992b, 11 pop.
Foliage blight resistance	: Tuber blight resistance	0.10-0.42	Swiezynski 1990, R-genes
Foliage blight resistance	: Tuber blight resistance	0.21-0.23	Swiezynski 1990, *dms*
Foliage blight resistance in field	: Tuber blight resistance	0.52, 0.27	Gundersen et al. 2000
Foliage blight resistance in field	: Tuber blight resistance	0.65	Platt & Tai 1998
Foliage blight resistance in field	: Tuber blight resistance	0.58, 0.35	Bradshaw et al. 1999
GCA foliage blight resistance	: GCA tuber blight resistance	0.56	Bradshaw et al. 1995b
Detached leaf test	: Tuber slice test	0.63	Durska 1975
Detached leaf test	: Whole tuber test	0.57	Durska 1975
Detached leaf test	: Tuber slice test	0.01-0.70	Swiezynski et al. 1997b
Natural field attack foliage	: Tuber slice test field-grown	0.47-0.62	Darsow unpublish. 1980
Foliage blight resistance in field	: Tuber slice test field-grown	0.15-0.80	Darsow 1992b, 11 pop.
Foliage blight resistance in field	: Seedlings tuber test	0.27-0.78	Darsow 1992a, 11 pop.
Foliage blight resistance in field, AUDPC	: Tuber test field-grown	0.27, 0.52	Gundersen 2000
Natural field attack foliage	: Tuber slice test field-grown	0.18-0.63	Darsow 1992b, 11 pop.
Seedlings tuber test greenhouse	: Tuber slice test field-grown	0.46-0.91	Darsow 1992a, 11 pop.
Seedlings tuber test greenhouse	: Tuber slice test field-grown	0.51-0.72	Oertel 1972, div. pop.
Seedlings tuber test greenhouse	: Tuber slice test field-grown	-0.19-0.72	Oertel 1972, div. pop.
Tuber slice test, field-grown material, two different years		0.48-0.81	Oertel 1972, div. material
Tuber slice test, field-grown material, two different races		0.30-0.85	Oertel 1972, div. material
Tuber slice test, field-grown, browning	: aerial mycelium	0.64-0.99	Oertel 1972, div. material
Tuber slice test, field-grown, browning	: aerial mycelium	0.74-0.90	Andreu et al. 2010
Tuber slice test, field-grown, different plants of the same clone		0.63-0.74	Oertel 1972, div. material
Tuber slice test, field-grown material, two different years		0.54-0.78	Darsow 1992a, 11 pop.

Traits, methods, conditions compared		r	Reference
Tuber blight resistance greenhouse-grown	: field-grown	0.67	Piotrowski et al. 1973
Tuber slice test, field-grown material, two different years		0.69-0.78	Piotrowski et al. 1973
Tuber slice test, field-grown material, two different years		0.09-0.55	Ratuszniak 1981/82
Undamaged whole tubers, % blighted tubers, lab test	: Field assessment	0.65	Flier et al. 2003a
Undamaged whole tubers, % blighted tubers	: Blight severity per tuber	0.88	Flier et al. 2001
Undamaged whole tubers, % blighted tubers	: Slice test, necrotic area	0.16	Flier et al. 2001
Undamaged whole tubers, % blighted tubers	: Slice test, area mycelium	0.36	Flier et al. 2001
Undamaged whole tuber test, blight severity	: Slice test, necrotic area	0.26	Flier et al. 2001
Undamagedwhole tuber test, blight severity	: Slice test, arial mycelium	0.33	Flier et al. 2001
Tuber slice test, necrotic area	: Area covered with mycelium	0.46	Flier et al. 2001
Seedlings tuber test greenhouse, browning	: aerial mycelium	0.71-0.31	Darsow 1992a, 11 pop.
Seedlings tuber test greenhouse	: Tuber slice test field-grown	0.81-0.51	Darsow 1992a, 11 pop.
Seedlings tuber test greenhouse	: Tuber slice test field-grown	0.87-0.40	Darsow 1992a, 11 pop.
Tuber blight resistance (overall), slice test	: Whole tuber test	0.05-0.21	Darsow 1983a
Whole tuber test	: Tuber slice test	0.29-0.44	Swiezynski et al. 1997b
Whole tuber test, growing in glasshouse	: Growing in field	0.72-0.93	Stewart et al. 1996
Whole tuber test, growing in glasshouse, two different years		0.74-0.95	Stewart et al. 1996
Whole tuber test, growing in the field, two different years		0.61-0.92	Stewart et al. 1996
Whole tubers, growing in glasshouse	: Foliage blight, field	0.46-0.69	Stewart et al. 1994
Whole tubers, growing in glasshouse	: Foliage blight, field	0.66-0.88	Stewart et al. 1994
Maturity	: Tuber resistance, 600 varieties	-0.46-0.41	Swiezynski 1990
Maturity	: Tuber slice test	0.11-0.38	Swiezynski et al. 1991
Components of foliage resistance	: Components of tuber resistance	0.06-0.73	Pietkiewicz 1976
Browning of inner tuber tissue	: Browning of tuber skin	0.43	Douches et al. 2002b

The cited correlation coefficients are calculated from different material, in different conditions with different methods. Very high correlations are untrustworthy and possible by choice of test material. For instance, Stewart et al. (1994) compared foliage and tuber resistance after assessing with only partly compatible inoculum and calculated the phenotypic correlation r = 0.72-0.93 for one set in one year, which of course resulted in overestimated genotypic correlation coefficients r = 0.74-0.95. However, in a diallel of ten clones tested two years the correlations between foliage and tuber scores for parents and for GCAs were not significant (Stewart et al. 1992).

2.9. Strategy of using host resistance

A question of strategy is the use of resistance in growing. There is a large difference in distribution of hosts and blight incidence between natural habitat and agriculture (Rivera-Pena 1990b, Flier et al. 2003b). Factors which wear out progress in plant breeding for resistance are: insufficient covering of refuse piles, narrow crop rotations or ignoring of rotation (Hannukkala et al. 2003b, Fernández-Pavía et al. 2004, Bødker et al. 2006, Deahl et al. 2009), incomplete prevention of groundkeepers, regional and/or on-farm concentration of potato growing, use of oomycides against which resistance in the *P. infestans* population is known (metalaxyl, propamocarb, dimethomorph, Wulfert & Scholz 1990, Salazar & Garcia 1999, Stein & Kirk 2004, Hannukkala et al. 2005), insufficient selection of blighted seed tubers, increased amount of nitrogen fertilizer, dominance of highly susceptible cultivars in growing, early crop under polythene, and other measures known to raise the danger of blight (Niederhauser 1991). Covering of early crop usually excludes long time application of oomycides and improves the conditions for the pathogen additionally. Such crops act as sources of inoculum for neighbouring potato fields. In the Netherlands the growing of the very susceptible cultivar Bintje has been increased from about 20% of the total potato acreage in 1951 to nearly 40% in the late 1980s, the area of potatoes per farm increased about threefold, and total hectarage of potato rose 15% during that period. The input of nitrogen rose twofold. At the same time effectiveness of late-blight control by fungicides increased at least 40%, which could not compensate the negative effect of mentioned changes in the following period, showing that control of *P. infestans* became not easier at present (Zwankhuizen & Zadoks 2002). The (man-made) changed conditions of potato production made that 18% of primary infections were caused by oospores in the northeast of the Netherlands and that up to 78% of leaflets with two or more lesions from volunteer potatoes had produced oospores, which survive at least five winters (Cooke et al. 2011a). Therefore crop rotation is necessary as measure against late blight too.

The highly susceptible and very old variety Russet Burbank still accounts for almost half of the potato acreage in the USA (Staples 2004) and causes very high infection pressure and requires weekly fungicide application. In case of reduction of other plant protection measures (absent or reduced crop rotation) only the few farms of high grade seed production will take the gain of resistance; in course of following year's seed tuber infections increase quicker than avoidable. Such development regulated by gain of highest profit at present runs in opposite to long-term gain because "durability can be ensured by adequate resistance management" (Zadoks 1993). Qualified use of oomycide dosage in time and choice of ingredient (Bødker & Nielsen 2001, Spits & Schepers 2001) is one point of good strategy of exploiting host resistance. To achieve control of late blight, it is essentially to exploit the range of all available control measures in an integrated programme.

New cultivars with higher quantitative resistance level of foliage will put in a long-term advantage for a region or country by lesser environmental pollution and more stable production, but frequently only, if increased tuber blight resistance exists at the same time.

It is known that effect and durability of resistance depend from distribution of cultivars in area and time. Regional dominance of one resistant cultivar over long time as Champion in Ireland supported adaptation of the pathogen to its quantitative resistance in past (Davidson 1928, Black 1947, Salaman 1949a, Latin et al. 1981). Champion covered in 1882-1884 regionally 80% of the potato acreage. Similar development was observed with Voran in northern part of the Netherlands (Toxopeus 1956a). However, instead of adaptation of the pathogen increased susceptibility of the host due to virus infections is an other explanation.

Mixed crop growing in a part of developing countries counteract this process. The middle dispersal gradient by sprinkled drops with spores of *P. infestans* and the high foliage area of single potato plants are expected to make mixed potato crop lesser effective than mixing of cereals (Mundt & Leonhard 1986). However, an advantage of growing in alternated rows was stated

by Andrivon and Lucas (1998) and is shown by Garrett and Mundt (2000) concerning foliage blight, tuber blight and yield. A random mix of cultivars of different levels of resistance, but similar maturity and purpose, however, different skin colours enables separation after harvest. In such manner selection pressure for increased pathogenicity should be reduced on the one hand and advantage of lower spore efflux from quantitative resistant cultivars is used on the other hand. It should be tried first line in organic farming (Finckh et al. 2007). The effect of host diversity is influenced by eco-climatic conditions (Garrett et al. 2001). Different sets of resistance genes in space and time are intended to apply by mixing cassettes of cis-genically modified cultivars within and between fields and regions using hypersensitive type of resistance in future too (so-called dynamic cultivars, Kessel et al. 2010). The idea corresponds to the RETONA-Project of Niederhauser (1993). The benefit from use of genetic diversity of resistance on each field in potato growing should not be underestimated (Dangl & Jones 2001). Quantitative resistance, oomycide application in reduced dosages and mixed growth compliment each other (Mundt et al. 2002).

3. Breeding for resistance to *Phytophthora infestans*

3.1. Breeding for quantitative late blight resistance in past

Varieties bred before the Irish potato famine, were largely lost due to its susceptibility to *P. infestans* (Salaman 1939). Few cultivars were lesser invaded as for instance Lord Henry in France (Kolbe 1999). Production of new varieties from seeds after open pollination or by crossing became common. First examples of success in conscious breeding for quantitative foliage blight resistance using *S. tuberosum* ssp. *tuberosum* (*tbr*) were Nichol's "Champion" in 1869 and the Irish "Skerry Blue" by the late 1800s (Black 1947, Salaman 1949a, 1949b, Glendinning 1983, Umaerus et al. 1983). Influenced by Darwin, already James Torbitt crossed cultivars and selected the seedlings on a location with frequently natural blight infections (Lehmann 1938a). In USA following cultivars were found to be least susceptible: Rustproof (Woods 1903), Sir Walter Raleigh, Rural New Yorker and Clay Rose (Green 1904), Dakota Red (Stuart 1905), Irish Cobbler and Green Mountain (Jones 1905); cvs. Evergreen, President and Sebago are named by Reddick and Mills (1939). In Europe at the beginning of the 20th century reduced late blight was mentioned on cvs. Evergood, Discovery, Royal Kidney, Northern Star, Sir John Llewelyn, King Edward VII, Eldorado, Factor, Mohort, Irene, Geheimrat Thiel, Professor Wohltmann, Boncza, Eigenheimer, Paul Krueger, Topas, Professor Maercker. Simultaneous tendency to lateness caused delayed development of crop and mainly fictitious resistance (Mueller 1931, 1953). Some cultivars as Robijn, Populair and Victor correspond to this type. Already Salaman (1931) mentioned that the advantage of cv. Champion resulted due to late maturity. Altogether the genetic basis for late blight resistance was very small in used potato cultivars; introduction of genes for late blight resistance after the Irish famine was insignificant up to the beginning of the 20th century (Berthault 1911, Mueller 1931, Simmonds 1969). Cultivars released before 1925 had tuber blight resistance ≤4 in the 1-9 scale of increased resistance (Carnegie & Cameron 2001). That means best resistance was a bit lower susceptibility.

More hope Stuart (1905) connected with crossing of highly resistant wild potato species with varieties followed by careful selection. On this way the period of using race-specific, qualitative blight resistance (hypersensitivity governed by R-genes) to *P. infestans* in potato began, which was gained in significance by pre-breeding in governmental institutes (Broili 1921). Quick and simple assessment of resistance and its simple inheritance enabled impressive progress in transfer of genes for resistance from wild potatoes to *tbr* and separation from simultaneous undesired alleles by backcrossing and strong selection (see table 1). It was possible to finish selection for resistance on foliage and tubers before planting of the second year in a clone life or, with lesser effort, before planting the third clone year (Schick 1932, Rudorf 1950). In 1930 the

message was given by Mueller that the problem of protecting potato against blight should be solved by breeding (Mueller 1930). Similar, foliage blight "immune" varieties were planned to be introduced from a number of sources by Reddick and Mills (1939). The optimism in Germany was damped in 1932 by occurrence of a new race overcoming main part of resistant breeding material (Schick 1932). First expeditions to collect *Solanum species* enabled search for sources of different R-genes (Schick & Lehmann 1936). On the other side, this back-stroke in breeding prompted to collect more resources and to evaluate late blight resistance of gene bank material (Black 1947). New varieties resistant to current races often were found to be susceptible shortly after release (Rudorf 1954). The period of using hypersensitivity continued mainly up to the end of 1960ies and finished with the judiciousness that the pathogens adaptation is quicker than breeding progress.

From about 1890 to 1914 the effort of breeding for late blight resistance additionally fell down because of increasing chemical plant protection with Bordeaux mixture (Millardet 1885, Tschirch 1893, Jones et al. 1912, Kolbe 1982/83) and the difficulty to combine polygenic resistance with the very high number of other desired traits and increasing demand for table potato quality (Salaman 1926). In this period several highly susceptible varieties as Bintje and Russet Burbank could therefore be released. However, besides the main stream of using R-genes, strive for better use of resources for quantitative resistance in *tbr* gene pool went on, for instance with cross combination of quantitative resistant cultivars Ekihirazu x Evergreen or Irish Cobbler (Reddick 1928a, b), named 'accumulative breeding' by Sidorov (1937). Combining of unrelated resistant parents resulted in higher percentage of resistant progeny and even in cross of highly susceptible Chippewa x Kathadin (susceptible) some seedlings with middle foliage blight resistance were selected (Stevenson et al. 1937). Regional distributed old varieties Steinthaler and Halbfruehe were found to be quantitative resistant in 1924 in Germany (Lehmann 1938a). Testing of cultivated relatives of *tbr* showed that only accessions of *Solanum tuberosum* ssp. *andigena* from Columbia, Bolivia, South and Central Peru had a quantitative level of foliage resistance (Sidorov 1937). Rarely remarks are to find concerning tuber blight resistance the first decades. However, a high level of resistance in tubers has been found in two very old cultivars: Bravo, released 1900 (NL) and Jubel, 1908 in Germany (Swiezynski 1988). Was this result more due to lucky chance?

At Toluca valley in Mexico Niederhauser started in 1953 to use consequently "field resistance" with quantitative resistance as a main part and R-genes, by breeding and selection in the centre of origin of late blight resistance (Niederhauser 1972, 1991) with naturally occurring of highest known pathogenic diversity (Niederhauser & Mills 1953, Niederhauser et al. 1954, Galindo & Gallegly 1960). More than 25 potato varieties with high level of resistance were released and some were grown for more than 30 years at Mexico and other countries (Niederhauser 1993). The need to reverse to quantitative resistance based breeding was emphasized by van der Plank (1956) too. Authorities in the field of breeding urged repeatedly more to take care of breeding for late blight resistance. Schick and Hopfe (1962) argued that in spite of oomycide application breeding of durable late blight resistant varieties is one of the most important tasks of potato breeding. However, the problems in using polygenic determined late blight resistance were underestimated. So Simmonds (1969 p. 27) wrote "In practice,… , blight resistance breeding is back at the point where the 19th century potato selectors left it, though we do now have a tolerably good understanding of the underlying scientific problems". These problems partly have not been solved, and moreover, the necessary public support was underestimated. The thinking in breeding was fixed on simple methods and simple inheritance and the willingness to apply much higher efforts in practice has been fallen down in the 'fungicide era'.

In 1954 Schick focussed on the quantitative resistance in the governmental Institute for Plant Breeding at Gross Luesewitz (Schick et al. 1958a, b, Darsow et al. 1989). Methods for assessment of foliage resistance on large scale (Haussdoerfer 1959a, b) and tuber resistance (Jeschke 1967)

were adapted and breeding was started on the basis of three new sources of resistance from *S. demissum* (Oertel 1972). The use of wild species to introduce additional genes for resistance was essentially; reach experiences from past were considered (Lehmann 1937, 1938a, Rudorf et al. 1950, Toxopeus 1964, Black 1970). Selection for blight resistance of tubers had priority. In the 1970s and 1980s the genetic basis of the material was continuously broadened by selected genotypes from accessions of the gene bank Gross Luesewitz (Darsow 2000b).

Other countries similar turned to the quantitative type of resistance by pre-breeding at public institutes (Black 1960, 1964, Melard 1964, Jacobsen 1964, Umaerus 1964, Wriedt 1974). Howard (1982) wrote: "There must have been more work on breeding for resistance to blight (*Phytophthora infestans*) than on breeding for resistance to any other pathogen." This statement is underlined by Robinson (1976): "Ironically, we have been least successful with the diseases that we have been the most intensively studied". Last more than 30 years using of a broad range of wild species as sources of (quantitative) resistance against late blight was intensified (Zhitlova 1987; Darsow & Hinze, 1991a, b, 1992; Wastie 1991, Rivera-Pena 1992, 1999, Colon 1994, Bradshaw et al., 1995a; Darsow 1995, Singh et al. 1999a, Stewart & Ramsay 1999, Micheletto et al. 2000, Douches et al. 2001, Kolobayev 2002, Jakuczun & Wasilewicz-Flis 2004, Thieme et al. 2005, Trognitz et al. 2005, Yakovleva et al. 2005). Frequently expectations and methods used were similar to practice in using of hypersensitivity. Very rarely long-term pre-breeding was planned; on the contrary, often it was expected that breeding can have sufficient gain from short research projects by the way. Only one scientific precondition for successful breeding was fulfilled from the beginning: sources of resistance were available. But the time required to breed new cultivars based on that sources is running according to table 1. In France parents from CIP and different countries were used instead of own programme with wild material (Rousselle et al. 1992, Marhadour et al. 2010). In Great Britain since Black no new sources were added for late blight resistance (Bradshaw 2009). The problem in using of quantitative late blight resistance from wild species in comparison to R-genes lies in its polygenic nature and distribution of resistance alleles (drop down of resistance level) with each backcross, which is most effectively to reduce the undesired "wild" alleles for many other traits (see chapter 6 and 7). Ross (1966) considered quantitative resistance alone doubtless to be not sufficient basic of resistance.

Yet, very light tendency of improved quantitative foliage blight resistance by breeding was stated by Zadina (1964c), who tested 486 cultivars of a world collection at Havlickuv Brod; in average of cultivars released before 1930, 1931-1940, 1941-1950, and 1951-1960 a continuously improving by about a half score (3.13-2.46) in a 1-5 scale increasing susceptibility was shown. Analysis of most resistant cultivars among 600 described by Stegemann and Schnick (1985), among 708 tested by Zadina (1964c), among 183 described by Hogen Esch and Zingstra (1962) and of the Polish collection by Jastrzebski and Budnik (1987) showed that the number of cultivars resistant in foliage increased in decades of varieties release before 1970 compared with the period after 1979, however such resistant in tubers remained similarly (Swiezynski 1988). Kapsa and Jastrzebski (1982) stated that cultivar breeders in Poland quite recently started to assess quantitative late blight resistance. Baetz (1979) found that during 25 years foliage blight resistance of western German (FRG) cultivars could be improved by 0.4 scores in a 1-9 scale. A tendency of improved quantitative blight resistance of tubers by about 15 year's cultivar breeding for resistance was described by Kleinhempel and Goetz (1982). According to the own tuber slice test only one third of the cultivars of GDR at the end of 1980ies had a quantitative tuber blight resistance ≥5 in the 1-9 scale of increased resistance, but in the variety list about two third were certificated with that level (Darsow et al. 1989). No any breeding progress stated van der Zaag (1978) for the Netherlands varieties since about 1960, whilst Swiezynski and Domanski (1998) showed a reduction or standstill for tuber blight resistance from Germany, the Netherlands and Poland in the period 1976-1996 in parallel to little progress in foliage blight resistance.

Darsow (1991b) showed clear differences concerning late blight resistance level of several

countries cultivars, but there is reasonable doubt that the methods applied entitle to direct comparison (table 8). Differences up to five scores occur between results of the same cultivar in the variety list of Great Britain and the Netherlands. Own assessment usually resulted several scores lesser with the lowest difference to the British list. Some results are given in Darsow (2000a). Swiezynski et al. (2001) found differences up to 8 scores in a 1-9 scale for the same variety in assessment of different European countries. Too good results have been offered because of methodical insufficiencies, mainly because of R-genes acting against a part of inoculum and the result is interpreted as horizontal resistance, and probably partly to push out public pressure on breeding. Wustman and Carnegie (2000) urged to develop standard methods for cultivar assessment to ensure a meaningful transfer of cultivar information between countries in Europe.

All variety candidates of Soviet Union had to be officially assessed for foliage blight resistance on Sakhalin (Far East) since 1975, but using of R-genes was continued there longer than in main part of Europe. The varieties Zarevo, Fitoftoroustoichivostiy, Talvik and Uralskiy are known as highly resistant on foliage, Kameraz 1 on tubers (Swiezynski 1988). More results are given by Chumakova & Loktina (1978), Osipova (1980), Patrikeyeva (1972, 1981), and Kremnyova (1985).

Table 8 Percentage of potato cultivars (%) susceptible (score 1-3) or resistant (score 7-9) to late blight in a scale 1-9 increasing resistance in national lists of six countries (Darsow 1991b).

Country	Source of data	Resistance level of varieties of official list to					
		Foliage blight		Tuber blight		Foliage and tuber blight	
		≤3	≥7	≤3	≥7	≤4	≥6
GB	Variety list 1986	18	8	36	10	42	14
NL	Variety list 1988	33	4	4	37	10	11
BRD	Variety list 1988	2	25	8	38	2	42
DDR	Variety list 1988	0	14	0	36	0	50
Poland	Schueler (1972)	22	7	20	0	31	4
SU	Schueler (1972)	29	25	10	51	23	41

Farmers in the developing countries have increased their share of world potato production from 10% in 1950 to roughly one-third in 1990 (Niederhauser 1993). Extension of potato growing increased importance of late blight with estimated losses of 30% (Anonymous 1993). CIP at Lima, Peru, supports potato research and breeding in that part of the world by producing of foliage blight resistant material for crossing, adaptation or direct release in diverse countries. Help for resistance breeding of developing countries was expected from such projects as PICTIPAPA (International Cooperative Potato Late Blight Program) initiated by Niederhauser (1993) in 1990. This project included promise to global cooperation in research, assessment of resistance and resistance breeding. In PICTIPAPA finally Mexico, USA, Canada, the Netherlands, Poland, and CIP worked together, later on Ireland and Denmark were involved. Besides some aspects the initial intension of Niederhauser that developing countries should participate on European breeding material with late blight resistance run aground; cultivar breeders were not willing to unpaid globalization.

Two global cooperative projects resulted from PICTIPAPA, GILB (Global Initiative Late Blight) as world wide open network, and CEEM (Cornell-Eastern Europe-Mexico) project in potato late blight control to solve problems of USA. International cooperation was the new step of this decade to combat the single most costly biotic constraint to global food production, *P. infes-*

tans. GILB was planned in research and breeding over about nine years and started in 1997. It was intended to improve horizontal resistance in both foliage and tubers with highest priority. Utilization of new sources of blight resistance and exchange of most resistant clones of Standard International Field Trails among national breeding programs should improve breeding output besides development of molecular tools for application in practical breeding programs and refining of testing methods for resistance. The time table was overload, the goals partly unrealistic and far from breeding practice. The problems to apply quantitative resistance were underestimated. Several other international projects were started as ECOPAPA to support use of quantitative blight resistance in regional cooperation.

In 1996-2001 the CEEM-project run, in which USA, Mexico, Poland, Russia and CIP took part to compliment the national Phytophthora-program of USA. The Netherlands were involved in a part concerning population genetics of *P. infestans*. Late blight pressure at that time increased in potato growing of USA (Fraser et al. 1995, Secor et al. 1995), protection based only on oomycide application, breeding for late blight resistance did not really happen (Douches et al. 2002a, 2004, Deahl et al. 2005). A great national initiative of USA against late blight was started in parallel for research and breeding with a budget of $36 million, whilst CEEM had a budget of $3.35 million over six years (Anonymous 1997). In CEEM know-how concerning assessment of blight resistance, transfer of tested sources of resistance, breeding material of different stages were taken over, and field assessment at the Toluca valley immediately could be carried out. One aim was to accelerate combining of late blight resistance with processing quality, nematode and scab resistance (Douches et al. 2001, Pavek & Corsini 2001).

In general, continuously improved possibilities of chemical plant protection up to the 1990ies decreased the readiness to pay several times higher expenditure for exploiting quantitative resistance compared with qualitative resistance, in view of not satisfying results. Ross (1986) summarized: "Although the history of resistance breeding in case of *Phytophthora infestans* is fascinating, its results are disappointing." Last century some British late blight resistant varieties were released, however none of them had sufficient table or processing quality for commercial success (Bradshaw 2009). Similarly Salaman (1926) resumed: "it must be admitted that of the varieties listed in "Potato varieties" none of them combine quality, cropping and blight resistance in any notable degree".

3.2. Late blight resistance in cultivar breeding today

Scientists of developing countries named late blight resistance highest priority need for potato breeding of developing world; demand for pre-breeding had a high priority too in a large survey (Fuglie 2007). Also demand for resistant potato cultivars for Europe is increasing (Cooke et al. 2011a).

Good results in breeding for quantitative resistance to late blight are known from CIP Lima, Peru (Estrada & Turkensteen 1978, Landeo 1999); and more than 60 cultivars in many countries trace back to its material (Zandstra 1999) by directly release after regional selection, mainly used in short day conditions in Africa (Wurster & Kori 1972, Nganga 1984, Demo et al. 1999, Hakiza 1999, Hakiza et al. 1999, Lungaho et al. 1999, Sengooba & Hakiza 1999), South America (Nustez 1999), but also in Asia (Wei et al. 1999). Very important is transfer of knowledge at the same time about potato growing, diseases, disease control, use of resistance and breeding. In GILB it was not intended to initiate pre-breeding outside of Peru but that is necessary in several of developing countries in cooperative manner for large regions. Breeding for blight resistance in Toluca valley, Mexico, uses directly the highest known naturally genetic diversity of pathogenicity of *P. infestans* for selection in the field (Rivera-Pena 2005); more than 24 cultivars are reported with partly good results (Rivera-Pena & Rubio-Covarrubias 1999, Lozoya-Saldaña & Hernandez, 2000, Gruenwald et al. 2002); some are tested in other regions with an effect of cultivar resistance (R-genes and quantitative resistance) equivalent to 2-8 oomycide applica-

tions (Cadena-Hinojosa et al. 2007). Ecuadorian potato breeding programme started in 1992 to use multigenic quantitative blight resistance with high priority (Andrade et al. 1999). Bolivia has own potato breeding.

Breeding for late blight resistance was aimed at quantitative resistance more consequently in the Indian programme after 1985 and has been successfully so far (Verma 1978, Singh et al. 1999a, Gaur & Pandey 1999, Anonymous 2000/01, Kumar et al. 2010). Two Indian cultivars belonged to the five most resistant late ones in foliage (Jastrzebski & Budnik 1987). Asian countries in sub-tropical climate do not have own potato breeding besides India (Singh 1999a). In China breeding for late blight resistance seems to stay in its infancy (Wei et al. 1999, Jansky et al. 2009a). Huarte (1999) informs about some success in Argentina, but some problems in breeding for durable resistance under long day conditions are not solved (Landeo 1999).

Resistant cultivars as Sarpo Mira and Axona from Sárpo Kft in Hungary have been listed in UK (Shaw et al. 2005); they have its origin in potato breeding at Keszthely, more than 45 years ago, with application of seedlings selection for resistance to late blight, to PVY and PVX and test of detached leaves in large scale (Sarvari 1964, 1982). The majority of 20 Sárpo-clones and cultivars tested in western UK was highly blight resistant (Kiezebrink & Shaw 2006, Shaw & White 2011). The genetic background of those cultivars is unknown (Shaw et al. 2005). Polgar (2001) as Cameron and Carnegie (2001) hinted at possessing R8 in some of that breeding material. An R-gene effect is confirmed besides quantitative resistance in Sarpo Mira (Tomczynska & Sliwka 2011). At the Scottish Crop Research Institute some cultivars with improved level of blight resistance were bred (Shelagh, Torridon, Brodick, Stirling), but only Lady Balfour had commercial success up till 2007 (Wastie 1991, Bradshaw et al. 1999, Bradshaw 2009). In Germany cultivar breeding is on the way to intensify the use of quantitative foliage blight resistance, but pays not (enough) attention to tuber blight resistance.

Eastern European countries focussed more attention to resistance with partly success on the long way of combining the many different traits (Kameraz 1964, Chumakova & Loktina 1978, Patrikeyeva 1981, Kremnyova 1985, Anoshenko 1999, Zimnoch-Guzowska 1999, Rogozina & Patrikeyeva 2004). Broad pre-breeding is reported from Ukraine (Podgayetsky 2000), Belarus (Yermishin et al. 2011) and Russia (Rogozina & Patrikeyeva 2004, Simakov et al. 2011). Russian breeding had central breeding, but selection of the progeny on diverse locations in parallel (Simakov et al. 2002). The recommendation to use of less attacked R5, R8, R9 differentials as sources of late blight resistance in breeding (Swiezynski et al. 2000b, Sieczka et al. 2001) expresses distrust of polygenic resistance too and underestimate the effect of lateness (see 2.5.). Most late blight resistant Polish varieties are late ones, as Bzura and Meduza (Zimnoch-Guzowska et al. 1999). Hungary combined successfully resistance to virus diseases with some blight resistance (Polgar 2001), but mainly susceptible cultivars from abroad are grown by farmers. Success in other countries is mostly on a lower level from different reasons. Some European countries stay at the beginning concerning late blight resistance (Petr & Pavlas 2000).

Nordic countries seem to start again with several selected sources from VIR St. Petersburg (Zoteyeva & Carlson-Nilsson 2011). The national "masterplan" for late blight of the Netherlands contained as long-term objectives that commercially interesting varieties should be late blight resistant. Revision of test procedures and increased activities of breeders were included (Schepers et al. 2000). The Netherlands decided then a national solo attempt in preparing use of R-genes by gene engineering (Jacobsen & Schouten 2008).

In USA extensive working is to obtain in pathology with modern methods, in resistance assessment and broad attempts of breeding using quantitative and qualitative resistance (Bisognin et al. 2002). However, the available knowledge from literature is partly not known and a lot of avoidable insufficiencies are repeated. In breeding the chances are expected too simple and very optimistically (Douches et al. 2001). Some research of last years could be saved. Coop-

erative effort in pre-breeding between USA and Canada are mentioned by Pavek and Corsini (2001).

Mutation breeding for late blight resistance used irradiation of nodes and internodes with X-rays and somaclonal variation of in vitro plantlets (Kowalski & Cassels 1999). One of 2101 clones during the experiments corresponded to the aim, but the method did not enter into breeding practice.

After decades a beginning of organic potato breeding is to mention (Lammerts van Bueren et al. 2008, 2010, Vergroesen et al. 2008, van der Zaag 2010), however not systematically and independently enough. Partly blight resistant cultivars as Appell, Naturella and Innovator are preferred in organic farming only in some regions, for instance in Switzerland (Hebeisen et al. 2002). Usually susceptible cultivars well known to the consumers are grown and offered, which are not enough suitable for organic farming.

The present practice of public assessment of cultivar resistance does not serve breeding for resistance. Already in 1989 own results showed that foliage blight resistance of some cultivars from Western as well as from Eastern European countries were up to 7 scores overestimated in a 1-9 scale (Darsow 1989c). A part of the difference with 3.5 scores in average of 34 cultivars was caused by a stronger measure applied in pre-breeding compared with cultivar breeding. However, in 2005 within 11 European countries inquired 341 varieties with foliage and/or tuber blight resistance score ≥6 in a scale 1-9 of increasing resistance were ascertained from the national lists (Zimnoch-Guzowska, personal communication 2005). That is in contrast to

1. the real input of breeding concerning blight resistance up to now, which is to low;
2. the degree of difficulty of the task, which enabled slow progress only from high input;
3. the applied methods of assessment of blight resistance in breeding, which are mainly not adequate and selection for blight resistance is applied in a stage, in which the majority of resistant progeny is eliminated because of other traits.

Table 9 shows a cutting of foliage and tuber blight resistance of cultivars, given in national lists of different countries, placed together in European project EUCABLIGHT (Zimnoch-Guzowska et al. 2005). For instance the cultivar Adora shows a range of foliage blight resistance from very susceptible to modest resistant. Swiezynski et al. (2000a, 2001) found differences up to eight scores in the scale 1-9 for tuber blight resistance for the same cultivar between European countries, with highest glossing over in national lists of the Netherlands and France. What will be the chance of breeding on the basis of such evaluation? "Often the current resistance figures according to the Dutch variety list seemed not to be appropriate" mentioned Wander et al. (2006).

Table 9 Cutting of a list of European cultivars with foliage (FBR) or tuber blight resistance (TBR) ≥6 in a scale 1-9 of increasing resistance in national lists of 11 countries, assorted by Zimnoch-Guzowska in European project EUCABLIGHT.

Cultivar	FBR TBR	Year of release	Country								
			FI	NO	PL	GE	SK	NL	UK	FR	Mean value
Adora	FBR	1990	6.0	-	-	-	4.0	1.0	-	3.0	3.5
	TBR		7.0	-	-	-	6.0	8.0	-	8.0	7.2
Agata	FBR	1990	-	-	-	-	3.0	5.0	-	4.0	4.0
	TBR		-	-	-	-	4.0	5.5	-	8.0	5.8
Agria	FBR	1985	-	-	-	6.0	4.0	5.5	-	4.0	4.9
	TBR		-	-	-		6.0	7.5	-	6.0	6.5

Glendinning (1983) stated that our modern varieties are still provided with about 80% of genes identically to the very narrow gene pool at the beginning of 20th century. Described level of resistance in the most topical variety lists would comply with optimistic hope after additionally 20-30 years of intensive use of best inheritors of blight resistance in a broad part of the breeding programmes, consequent application of recommended methods of assessment (at minimum according to the protocols of the EUCABLIGHT project given in www.eucablight.org) and changed selection scheme (see chapter 4 and 6). Therefore this currently high number of "resistant" cultivars is a sign of insufficient quality of assessment or/and of palliation at present. Up to now in main part of Europe and North America the most important or nearly only measure against late blight is application of oomycides. In some countries there is a tendency to reduce the fungicide input, however, in most countries not (Hannukkala et al. 2003a, Schepers & Spits 2006, Brendler et al. 2007). The attempts by commercial breeders for late blight resistance are predominantly insufficiently.

Active use of polygenic resistance to late blight is in many breeding enterprises saved up till now. Partly negative experience has been accumulated. Often the required knowledge is absent how to improve quantitative blight resistance in the right manner. Late blight resistance originates from wild species, but its introgression by breeding is usually tried by backcrossing which is after BC3 not the right manner and therefore is assumed that "likely resistance genes are linked to genes negatively affecting tuber quality" (Swiezynski & Zimnoch-Guzowska 2001). The board of EAPR required more research on quantitative late blight resistance in 1981 to support breeding for resistance (Anonym 1981) but little has been done. Allefs et al. (2005) established: "Under long day conditions race non-specific resistance is strongly correlated with foliar maturity" (a principle wrong statement as is explained in 2.5. and 4.2.4.). They concluded for breeding : "We consider maturity related resistance (here synonym for quantitative resistance, Darsow) inadequate for substantial contribution to integrated late blight management strategies under long day conditions and think that exploration of R-genes ultimately could prove to be the better option." These arguments support the decision for a "Netherlands Initiative on Late Blight" (NILB or DuRPh, 2003-2012, budget of 10 Million €) to detect and use new R-genes from *Solanaceae* for modification of known cultivars by gene engineering (cis-genic crops without alien genes, Jacobsen & Schouten 2008). Genes from *S. bulbocastanum* with assumed broader spectrum of defence are intended to use combined with other R-genes in a system of gene stacking and variably spatial and temporal growing of patented varieties (Anonym 2006, Haverkort et al. 2009, Kessel et al. 2010). Allefs et al. (2005) display optimism: "…we conclude that breeding for late blight resistance in potato has only just begun". Scientists and breeders prefer dominant genes, simple selection and simple reactions in molecular genetics. However,

Mackay (2000) advised to transform such constructs into naturally, partly resistant genotypes instead into susceptible cultivars. That intended Gonzales-Virgil et al. (2005).

3.3. Causes of insufficient results in cultivar breeding for late blight resistance up till now

Much work has been done for late blight resistance last decades too, but its efficiency seems in majority to be very low. Breeding for late blight resistance is very difficult and in many countries it was saved during decades; an extreme example is USA (Douches et al. 2002a). Besides highly intensive use of oomycides several arguments can be advanced for insufficient progress in resistance breeding on quantitative basis. According to Robinson (1976) phytopathology was not enough engaged in population dynamics of *P. infestans* and breeding research not enough in crop-pathosystem interaction to get the right measure for resistance to future epidemics; and this future means next 20-30 year's. Public research institutes in Europe are moving away from applied potato research; private breeders do not enough bring in their own support to ensure improved practical solutions (Bonnel 2008).

Four pre-conditions have to be fulfilled to enable breeding success: 1. a clear breeding objective, 2. suitable material, 3. reliable and quick assessment methods, 4. protective propagation of selected breeding material (Schick 1956). In using quantitative late blight resistance the breeding objective should be clear. Suitable sources of resistance are amply available in gene banks. From other traits as quantitative virus resistance (PVY, PLRV) the consequences from its polygenic nature for the breeding method are known. However, the difference is sources here are wild species and parental clones for exploiting in variety breeding have time-consuming to be developed (see table 1); the ability for that continuously has been decreased from past because of several reasons (chapter 10.3.). The necessary pre-breeding is difficult, labour-intensive and protracted. It has not been done due too a lack of judiciousness, willingness or because of monetary reason (Pavek & Corsini 2001, Fuglie 2007). From literature high priority for quantitative late blight resistance is only consistently realized by CIP (Zandstra 1996, Sieczka et al. 1992) and at Gross Luesewitz. One messages from breeding research for using of quantitative resistance last decades was considering the genotype (GCA) instead of phenotype in selection (Bradshaw & Mackay 1994), and another to hope for genetic engineering (Mackay 1996). Breeding practice relevant results at ZL Gross Luesewitz (Darsow 1987a, 1988b, 1989b, 1993, 1995, 1998a, 1999, 2000a, b, c, 2002a, b, 2003b, 2005a, b, 2006, 2008) did increase interest in material transfer but apparently did not influence applied breeding strategy and expenditures to improve the quality of selection for late blight resistance in other countries.

Potato breeding is clone breeding, but for improving of polygenic determined resistance population breeding would be more appropriate (Robinson 1976, Foldø 1987). Some successive examples are known (Simmonds & Malcolmson 1967, Simmonds 1969, Mendoza 1987, Plaisted et al. 1987, Glendinning 1989, Tarn et al. 1990), but not consequently with orientation to supplement variety breeding and adapt its measures. Alternatively is necessary to prefer crossing resistant x resistant instead of poor backcrossing. In case of blight resistance such system requires much higher demand because of

1. the long breeding way from beginning with wild species,
2. considering at the same time foliage and tuber blight, and
3. having only low progress in coming back to the variety level regarding the many other traits which deteriorated due to crossing with wild species.

Whilst monogenic dominant R-genes are easy to remain in a breeding stock, polygenes for resistance are distributed in meiosis to the progeny; in case of clone breeding they are partly lost by selection; counter-measure is inter-crossing resistant x resistant. For that, it is necessary

to establish pre-breeding between applied science and cultivar breeding. However, even institutes of breeding or breeding research usually are not able to keep more than a small working collection (Foldø 1987). The true reason of insufficient results is the lack of a frame that enabled purposefully complex long-term pre-breeding aimed at needs of cultivar breeding. However, there is no other way to realize the social intention or willingness to more consequent pollution control. Private or governmental variety breeding can not take over this task according to own opinion, literature (Ross 1986, Foldø 1987, Pavek & Corsini 2001) and opinion of cultivar breeders.

Currently the following aspects are mentioned as bottle-necks in breeding for late blight resistance: 1. agronomic value of used resistance sources, 2. combination of resistance and earliness, 3. complexity of genetic determination of blight resistance, 4. combining of foliage and tuber resistance, 5. available methods of resistance evaluation, 6. cost of selection, 7. lack of molecular markers (Zimnoch-Guzowska & Tatarowska, 2004). These points underline that breeding based on quantitative resistance here has its highest difficult task. Bottle-necks 1-5 mentioned are sufficient known since more than 50 years and the old literature comprises amazing many helpful information for practical solutions. The problems connected with these bottle-necks mainly could had been solved or reduced by decisions in time. Financial arguments are used mainly because of lack of strategic decision. Marker-assisted selection (MAS) is not a pre-condition and will not be applied for quantitative late blight resistance probably next 10 years. That period science needs to work more intensively to increase its applicability.

The level of resistance is a question of the number of genes joined in, its load and of its interactions. Yet, alleles occur on each of four nearly identical chromosomes. Pure potato lines are rarely obtained due to serve strong inbreeding depression. Tetrasomic inheritance does not enable genetically to interpret phenotypic results of a progeny, in which more than three minor genes are involved. More complicated is the situation, if use of wild species in the parentage leads to partly or segmental allotetraploids, so that departures from expected Mendelian ratios through non-random pairing of chromosomes can not be ruled out (Mueller 1930, Black 1952, Bradshaw 1994, Sliwka et al. 2006a).

Reliable assessment methods are another crucial point. Environmental influence often has the consequence of significant interactions as cultivar x location or cultivar x year (see 2.3., 2.7., 2.8.); some examples are given by Forbes and Landeo (2006) and Huarte (1999). Minor genes cause small effects and require much higher effort (more plant material, several test dates, several inoculum densities, several dates of observation, more complicated calculations of a result) to assess blight resistance. Additionally, experience of the person estimating the disease level on a quantitative scale plays an underestimated rule. Extensive practice is required visually to distinguish small differences repeated and sure; and only in this manner breeding material can be screened in large scale up to now and in future. Generally underestimation of personal faculty and overestimation of scientific impression cause additionally inefficiency in resistance assessment and breeding for late blight resistance. In North America and in main parts of Europe the expenditure of work for qualified assessment of quantitative resistance on foliage and tubers in breeding seems difficult to achieve.

Late attacked very late cultivars as Robijn are falsely described as highly quantitative resistant. They require high number of oomycide applications, independent of their 'high resistance' (Hansen et al. 2002a). Foliage blight resistance is usually assessed with methods, which do not separate the small part of true quantitative resistance from the larger effect of lateness on the disease progress curve of breeding material as well as wild potato clones. That problem was already perceived by Mueller (1930) and is considered in 2.5., and methodical details are given in chapter 4. Lack of cooperation between pathology, physiology and breeding did not enable a qualified methodical solution and did not result in realistic valuation of the potential of quantitative late blight resistance. Therefore unsuitable or inadequate methods of assessment

of foliage blight resistance predominate globally today.

Quantitative resistance is commonly on low to very low level in cultivars and in cultivated potato species, and up to a very high level in a part of wild species, and there in a part of individuals only. Frequently any level of quantitative resistance occurs together with qualitative resistance (R-genes) in the same clone. Then the last can exclude a main part of inoculum (depending from its virulence gene combinations) or attack at all; the result may be interpreted wrong to be caused by quantitative resistance only. A widely accepted opinion considered all late blight resistance to be valuable. That is true for its action in potato growing and a reason to use combination of quantitative and qualitative resistance in breeding instead of abandoning the R-genes. However, a breeder has to know which type of resistance exists in each of his clones. It is a tricky methodical question to use compatible inoculum to assess the true level of quantitative resistance. Only reliable results enable the right cross planning to improve the level of durable resistance or to hinder its strong falling down in combination of resistance with quality and earliness. A special case is selection of wild species as sources of blight resistance, in which it often is not possible to recognize, which type of resistance is present, very high quantitative resistance or mainly an unknown R-gene effect. Analyse of interspecific crosses with cultivars or first backcross enables the answer. In that case use of the maximal known virulence gene combination is necessary in the pathogen inoculum for assessment of resistance and ensuring optimal conditions for the pathogen.

Quite insufficient is however, that resistance of foliage in the field is mainly tested with local races (without inoculation) and without making sure compatible host/pathogen relationship for the whole material. So some R-genes can have been reduced (filtered) the quantitatively active (pathogenic) part of the pathogen population, slow down temporary or delay disease progress and pretend quantitative resistance of some clones, which is greatly overrated and later proved to be rather susceptible. Examples are the cultivars Atzimba, Brodick, Maritta, Multa, Karnico, Kuras, Kufri Jyoti, Vertifolia and some wild clones (van der Plank 1963, Swiezynski et al. 1991, Turkensteen 1993, Clayton & Shattock 1995, Hansen et al. 2002b, 2005, Gopal & Singh 2003/4, Wander et al. 2006). Frequently 'successes' of field resistance are temporary because of a mixed effect of qualitative and quantitative resistance and insufficient methods (Turkensteen 1993). The effect of R-genes has to be excluded in assessment of quantitative resistance as far as possible by testing with an isolate that is able to overcome all known R-genes in material intended to test, perhaps with most complex virulent isolates from Mexico. Necessary investigations (disease onset and progress supported by irrigation and sheltering from wind) and required personal efforts are rarely realized. Such resolution is at present in majority not fulfilled, moreover, it is usually excluded by breeding enterprises because of danger from undesired infections by blowing out of spores from the special test field. Therefore common observation of natural disease progress or use of local race produces results with insufficient differentiation (examples in www.eucablight.org, and Swiezynski et al. 1991, Sieczka et al. 1992, Pavek & Corsini 2001) and improved risk for wrong selection and missing breeding success. Only growing on centres of pathogenic diversity as Toluca valley or perhaps the former station on Sakhalin (Far East of Russia, Loktina 1969) enables assessment and correct selection after naturally infection.

Compatibility of used inoculum with cross parents of breeding material is expected to lead to compatibility of its progeny to the same isolate. However, modifier genes can a present R-gene switch off, which may be rendered effective to some plants of the next generation by separation from the R-gene and cause in these unexpected good results (El-Kharbotly et al. 1996). How often this occurs is not known.

The demand of decades of years (table 1) to transfer quantitative blight resistance from wild species into cultivated level of trait expression calls for especially careful planning of cross steps (see chapter 5 and 6), but the opposite usually occurs at the beginning by a quick series of backcrosses. However, each crossing results in split up of complex of polygenes of the donor

to individuals of progeny. Therefore stepwise falling down of the resistance level is the result in backcrossing. Crossing of resistant x resistant alternated with backcrossing is necessary. That requires diverse resistant cross parents combined with suitable level of other desired traits, which is usually absent.

Assessment of blight resistance and pre-selection for it should be finished in rough outlines at the first three years after sowing, and more compromises concerning other traits are necessary to remain the best polygenic resistant clones and select between them for other traits in the following time instead of in reverse order (Parlevliet 1993, Darsow 2000a). Final selection for foliage and tuber blight resistance requires additional two to three years. Qualitative traits as resistance to nematode Ro1, for instance, can easily be introduced by the last cross before expected variety-level, with another blight and nematode-resistant cross parent. Frequent insufficiencies in breeding are selection for quantitative late blight resistance based only on single year's results and applying of only backcrossing to combine resistance with quality (see chapter 5-8).

In Germany the quality of field assessment for foliage blight resistance long time was pronounced better in some German breeding enterprises than in national evaluation of cultivar candidates by Federal Office of Plant Varieties (Bundessortenamt). Tuber blight resistance is there not evaluated since 18 years and usually not assessed by breeding enterprises. Such circumstances enable only partly to exhaust the potential of quantitative blight resistant prebreeding material of ZL by cultivar breeders and to select new cultivars, which require a third lesser oomycide supply.

Keeping pre-breeding material free from virus diseases is a pre-condition which is often not considered and often not possible because of unsuitable conditions; loss of the material is the not planned consequence.

Last about 20 years showed that there is a need for internationally concentrated, well coordinated effort not only for research, but also for assessing foliage and tuber blight resistance in gene banks and breeding, and mainly for pre-breeding (Mackay 2000, Colon et al. 2005, Zimnoch-Guzowska et al. 2005).

3.4. Potential of quantitative late blight resistance and pre-conditions

Improved quantitative late blight resistance is globally required. It has been used more extensively in developing countries (Forbes 2001), mainly based on breeding at CIP. For short day conditions the influence of maturity on foliage blight development plays not such a part as under long day conditions and is therefore simpler. That supports hopeful developing of breeding in short day conditions of Africa, South and Middle America and Asia. With breeding in Europe and North America it goes hardly to use quantitative late blight resistance because of economical reason (labour-intensively). Usually its potential is clear underestimated because of too short experience with it in breeding enterprises and most institutes. Nevertheless, Bradshaw (2007a, p.173) wrote "it does seem worthwhile trying to combine quantitative resistance with the other traits required for commercial success, such as early maturity, yield and the demanding quality specifications in developed countries". At ZL Gross Luesewitz this has been done quite systematically since 47 years (Darsow 1989c, 1990, 2008). Mackay (2000) requested to increase selection efficiency for late blight resistance. Our methods represented an important step in that.

The International Potato Centre in Lima reduced a part of the difficulties by eliminating known R-genes from breeding material (Landeo 1987, 1999, 2002, Landeo et al. 1995, Forbes & Landeo 2006). That allows testing for durable resistance world-wide without any compatibility problems, besides unknown R-genes are unexpected involved. At SCRI Dundee going on without R-genes was discussed (Wastie 1991).

Breeding for quantitative resistance requires a long-term concept, patience and high labour

intensity for slow progress to combine quantitative resistance from wild species with about 70 other traits, 25 years ago about 50 traits were mentioned to consider (Ross 1986). The results of ZL Gross Luesewitz show: All traits are combinable with quantitative resistance to *P. infestans* in desirable manner by conventional breeding (see 4.2., 4.4., 5. and 7.). The more traits are considered, the longer is the working period and the higher is the risk of failure. Breeding enterprises are overcharged, if improving of quantitative resistance is not permanent attended by governmental paid pre-breeding, which has to work at minimum 25-30 years in advance before cultivar breeding may material take over and use it. Sure results may be planned independent from patentees.

The following two figures show that chances of breeding progress are good as well from the side of the methods as concerning the used material in four representative cross families. Highly qualified practical performance of foliage blight assessment with small plots (only four plants) and two replications over three years gave very trustworthy results after 2-3 years (fig. 8, fig. 9). The data of Truberg et al. (2010) are based on AUDPC expressed on trail mean basis of four populations with 854 genotypes altogether. The expenditure in trail area and time is not too high on one or two places in cooperative pre-breeding for whole Europe (see chapter 9.2.).

The EU-project „Potato late blight network for Europe", EUCABLIGHT, was helpfully as first step for standardization of methods of estimation of host resistance and pathogenicity in Europe (Colon et al. 2005, Zimnoch-Guzowska et al. 2005, www.eucablight.org). Calculation of quantitative foliage blight resistance from primary data was further developed in the project and carried out on nearly latest scientific knowledge in Denmark (Hansen et al. 2006a, b). However, this integrative work should be continued.

Host resistance is often mentioned as most economic and most environmental-friendly measure of plant protection in potato growing (Douches et al. 2001). However, improving of the quantitative late blight resistance level will cause about the double price of a new variety from conventional breeding compared to susceptible ones. Indeed, blight resistance is the socially most desirable measure of protection (de Bruyn 1951, Stroykov 1974, Mackay 2000), but the most difficult one.

4. Methods

4.1. Methods of assessment of foliage blight resistance

Substantial methodical experience was developed in assessment of hypersensitivity to *P. infestans* (Schick & Lehmann 1936, Toxopeus 1954, Mueller et al. 1955). Inoculation of very young seedlings on moist filter paper (Kameraz & Kiselyov 1966) or seedlings in stage of two leaves (Mueller 1925, Schick & Lehmann 1936) or in stage of 4-6 leaves (Schick & Schaper 1936, Stelzner & Lehmann 1944) are known. Plants cultivated from stem cuttings (Schick 1932), sprouts (Mueller et al. 1955, Filippov & Ivanchenko 1964) or excised tuber buds (Melhus 1914) were inoculated as whole plants or detached leaves or leave discs (Hodgson 1962). Methodical progress rationalized isolation and culture of the pathogen (Schick & Lehmann 1936, Snieszko et al. 1947, Mueller et al. 1955). During the first half of the last century a lot of knowledge concerning quantitative resistance to *P. infestans* was elaborated and components of resistance subdivided, assessed and partly used in breeding (Vowinckel 1926, Lehmann 1938a, b, Huettenbach 1951, Rudorf & Schaper 1951). Cultivars were assessed already in quantity by Koeck (1931), Sidorov (1937), Stevenson et al. (1937), and Schaper (1949).

The effects of oomycides and of quantitative host resistance complement each other; reduced infection efficiency, reduced rates of lesion expansion and sporulation have been demonstrated with both (van der Plank 1968, Fry 1975). Some research done to study oomycide application efficiency brings simultaneously partly useful information for aspects of host resistance

(Schepers 1996). Important measures of plant protection are considered in decision support systems for integrated control of late blight (Schepers 2004b), which include host resistance.

Extensive literature describes methods for assessment of quantitative foliage blight resistance. In opposite to qualitative resistance not only one simple reaction (sporulation) is alternatively to register, but quantitative level of different aspects (components) of disease course may be recorded, depending from the aim of assessment (research or selection in breeding) and material (cultivar level, pre-breeding or wild species). The real priority of late blight resistance among the traits decides the intended degree of accuracy and consequently the applied methodical expenditure. To discern small differences in resistance, good screening and assessment methods are necessary (Parlevliet 1993). For practical breeding this decision is very difficult and mainly for that purpose this script intended to summarize the present knowledge and to support an appropriate solution. High influence of environmental and ontogenic factors requires standardization of these factors during test to get high reproducibility. However, conditions before inoculation should be representative for intended growing regions of a cultivar in the field and these vary in progressive range. Therefore statistical analysis of repeated tests from different locations and/or years only enables appropriate selection decision (Darsow 1987a, Darsow et al. 1988).

The methods can be subdivided according to the environmental conditions during the test, which may carried out in the field (Malcolmson 1976, Cruikshank et al. 1982, Dowley et al. 1999), in the greenhouse (Black 1964, 1970, Guzman-N. 1964, Filippov & Ivanchenko 1964, Umaerus 1964, 1969b, Simmonds & Malcolmson 1967) or in the laboratory (Vowinckel 1926, Hodgson 1961, Umaerus & Lihnell 1976, Goth & Keane 1997). Field assessment has the problem of only limited influencing the meteorological conditions for suitable disease progress. A stable, highly reproducible result of foliage or tuber incidence with a very simple method on only one date of assessment is possible for qualitative resistance, however, in principle not for quantitative resistance. The reasons are already explained: 1. intricate interplay of pathogen, environment and host, 2. requirement of separation of maturity effect from disease level to get the trait true resistance. The second point is rarely realized in described and applied methods.

Incubation in a moist chamber may be designed in very different manner, from Petri dishes, 100% closed plastic boxes (Porter et al. 2004) or test tubes (Goth & Keane 1997) to a greenhouse wetted by steam in intervals (Garcia et al. 1977, Krupinsky & Scharen 1983). However, one should mind that *P. infestans* reacts susceptible to increased levels of carbon dioxide (Zan 1962, Henniger 1966). Harrison and Lowe (1989) showed higher sporangia production with increased air change at ≥95% relative air humidity. Harrison et al. (1994) passed two litres of air per minute through the test chamber. Boxes which are not sealed should be preferred.

Some principles are valid for all test methods. Concerning isolation of ontogenically and environmentally caused effects on resistance some factors with a lot of references are mentioned in chapter 2.4. One has to take care for comparability of the plant material intended to assess. It is difficult from wild species or very diverse pre-breeding material to get comparable leaves for late blight assessment. Different treatments before planting of tubers to finish dormancy or earlier planting of late maturing material are possible. However, usually in the field assessment of foliage blight resistance disease level is preferred to observe on many dates and maturity differences are excluded later by calculation. In seedlings selection slower disease progress results from delayed inoculation. The test of detached leaflets requires use the same leaf insertion from all potato clones tested; in case of uneven development too young plants should be assessed on a later date.

Results are comparable only if the same environmental conditions existed before and after inoculation for material compared. Literature of chapter 2.4. can serve to inform about effects of the factors tested. How convenient and reliable is screening for quantitative resistance of seedlings grown in greenhouse? One has to make the own experience with it.

Quantitative foliage blight resistance requires compatible host-pathogen interaction. That means assessment with an isolate (or mix of few) virulent (potentially pathogen) to all tested clones. Most evaluations do not comply with this pre-condition because of using accidental local races and having R-genes in test material. Impression of good level of quantitative resistance is possible by incomplete defence due to a weak R-gene, by inoculum dilution owing to defence against the incompatible part of the spore-load, by retardation of disease because of small proportion of compatible inoculum part or later development of compatible races (Turkensteen 1989). Selection of a representative isolate or standard isolate for assessment of breeding material is questionable according to Carlisle et al. (2002) because of the cultivar-isolate interaction in all components of resistance. No one isolate was most aggressive in all components. In case of using one isolate one has to know the current situation of pathotype distribution and change after few years to a new high aggressive isolate with complex virulence as have been done by Carnegie et al. (2011). It makes no sense to select the isolate for inoculation on highly susceptible cultivars. Carlisle et al. (2002) recommended selection of suitable isolates with detached leave test on material with a broad range of resistance.

The inoculum may be prepared from culture of *P. infestans* on different culture mediums (Henniger 1963), on leaves or on tuber slices, from stored isolates or freshly collected ones, with different results. Therefore, from agar culture or storage 2-3 passages on tuber slices or leaves are recommended to check and restore a sufficient level of fitness and pathogenicity. The sporangia are collected in sterile distilled water; by subsequent filtering through gauze with 30µ and 10µ mesh width mycelium and bacteria are separated from the sporangia. Quantitative resistance requires quantitative adequate inoculum density (Lapwood & MacKee 1966, Warren et al. 1971, Yashina & Erochina 1977, Kroll & Eide 1981), which has to be adapted in its density (dosage) for each test period new, if optimal differentiation of testing material is intended. In practice pre-test at the beginning of a test series with standards should be conducted. Adaptation in the following weeks considers in case of foliage short-term changing of sunshine duration and temperature according to several years experience. Howard (1982) remarked: "It is necessary to monitor the tests so as to be absolutely certain that they are neither too sever nor too lax."

Zoospores germinate in 1-3 hours after its release from sporangia and enable in best manner uniform start of disease in assessment of resistance (Umaerus 1969a). A clean inoculum may be prepared by washing the leaflets with sporangia and collect the spores on 10 µm nylon filter cloth. After re-suspension the density can be adjusted on number of sporangia per ml (counted before or in parallel to release of zoospores) or of zoospores (counted after release of zoospores out of sporangia at 5-12°C after about two hours) with a haemocytometer in ten replications. Adjusted zoospore suspension should be placed at <11°C in separated equal parts, if inoculation of potato material requires several hours. Zoospores remain motile longer than eight hours, if 1 % potato tuber extract is added (McKee 1964). For that 300g of sliced potatoes are boiled 20 minutes in one litre water; the clear liquidise used after settling. Understanding of different physical and biological properties of zoospores and sporangia is necessary to avoid high error variance in assessment (avoid precipitation of sporangia during its sampling for counting; ensure uniform distribution of zoospores in the suspension and inoculum). Inoculation in daylight is to prefer; darkness is known to hamper spore germination (Russel 1978). Adaptation to the material tested is also possible by changing the duration of the inoculum drop before drying.

Studies with mixtures of *P. infestans* races indicated the presence of antagonism according to Malcolmson (1974/75). However, if one intended to counteract the quantitative cultivar-isolate interaction in quantitative resistance, mix of few isolates, from which each is compatible to all potato clones intended to be tested, in one inoculum is the simplest way. For breeding purpose mix of 2-3 isolates of highest available virulence gene combination considers the interaction

and increases the probability to include additional unknown virulence genes. A mixture of pathotypes which are not each compatible to all clones tested gives wrong results (Stewart et al. 2001a, b).

An impressive technical solution of suitable quantitative inoculation (quantitative inoculator with timer, atomizer and different target frames) is applied by Umaerus and Lihnell (1976). Best differentiation of tested clones occurs in case of best adapted inoculum density on a part of test material (Harrison et al. 1994). This part of highest interest is in cultivar breeding on a lower level (score 5-7) than in pre-breeding (score 6-8) and is to adjust to standard clones (cultivars). The best differentiation should be focussed on the level of resistance near the selection border to susceptible. Better than a fixed inoculum density is yearly adaptation according to the results of a pre-test. Additionally one can apply two inoculum densities in parallel and decide by means of the results to use only the high or the low density or the average of both for calculation of the level of resistance (own practice). Kroll and Eide (1981) used transformed dose-response curves as criterion of quantitative foliage blight resistance. Parlevliet (1983a) recommended to select against susceptibility and to support recombination on a middle level. Negative selection in early live stage of the potato genotypes is much more appropriate for quantitative resistance than positive selection. Strong selection is adequate for hypersensitive response.

The intensity of disease was earlier assessed as rough groups ore scores in scales 0-4 (Guzman-N. 1964), 0-5 (Popkova & Bychenkova 1968), 1-9 (Malcolmson 1976) or other. More commonly became estimation of percentage foliage area affected by blight every 2-4 days which can be converted to apparent infection rate r or AUDPC or final disease rating as measure of blight incidence. Clayton and Shattock (1995) compared the three calculations and found AUDPC most appropriately. Some authors used the duration from 50% incidence to 75% incidence as criterion of quantitative resistance (see Umaerus 1987). Zadoks (1972) recommended expressing the disease level relative to a well known standard cultivar. Determination of blight incidence is the first step, calculation of resistance the next. A score in a 1-9 scale is preferred by breeders as measure of resistance. More details are considered later. Components of active resistance and factors affecting passively the development of foliage blight operate simultaneously with changing relations in different plant stages. Generally the level of resistance of the potato material tested and its genetic variance should determine the choice of method of assessing, the density of inoculum and plant stage tested. For instance, it is to consider that architecture and physiological status of plants in greenhouse and field from in vitro plantlets differ from such growing from seed tubers. Young seedlings are much more susceptible than elder ones. Pre-breeding material with higher genomic part of wild species should have a higher variation in the resistance level than material of cultivar breeding.

Different scales are used to assess disease level with different arguments (table 10). Mathematical correctness underlies sinusoidal transformation of percentage to scores which requires the same little distances at the beginning of disease at the end of it. However, of practical interest is to discriminate small quantitative differences at the beginning of disease and follow exponential development with increased critical difference up to disease level of about 70%; the following part remains largely outside of breeder's interest. Therefore we avoid scales with to roughly steps in the part of highest interest and unnecessary fine differentiation at very high disease level.

Table 10 Scales for estimation of disease level

Score	9	8	7	6	5	4	3	2	1
Barratt & Horsfall (changed)	0	4	12	25	50	75	88	96	100
Darsow, field plot foliage	0	1.7	9.4	26.2	45.2	64.2	83	96.4	100
Cruickshank et al. (1982)	0	≤10	11-25	26-40	41-60	61-70	71-80	81-90	>90
BMS key, Cox & Large 1960	0	0.1	1	5	25	50	75	95	100
Oertel (1972)	0	1-10	10-20	20-40	40-60	60-80	80-90	90-98	>98
Sieczka (2001), field plot	0.2	1.1	4.7	18.3	50	81.7	95.3	98.9	99.8
Zarzyzka (2001a), detached leaf	0	3	3 . 1 - 10	10.1-25	25.1-75	75.1-90	90.1-97	97.1-99	>99
Estrada-Ramos et al. (1983)	100	97	90	75	50	25	10	3	0
Henfling (1982)	100-97.1	97-91	90-75	74-50	49-25	24-10.1	10-3.1	3-1.1	<1.1

In all cases results of standard cultivars or well known clones help to rate a method. Already Schick and Lehmann (1936) used standard clones for methodical control. Table 11 shows some cultivars recommended by Section Pathology of EAPR as standards for foliage blight assessment in first column and own results in average of two to three years at Gross Luesewitz (GL). We recommend standards with a relative low clone-year interaction and clone-location interaction and intend its long-term use.

Table 11 Recommended standard cultivars according to Dowley et al. (1999) and own results at BAZ Gross Luesewitz (GL) in field assessment, single leaf test and whole tuber test, increasing resistance in the scale 1-9.

		Resistance on foliage as result of			Resistance of
Maturity	Cultivar	Dowley et al.	Field test at GL	Leaf test GL	tubers GL
Early	Gloria	6	3	4	5
	Jaerla	6	3	2	-
	Eersteling	2	2	3	-
Second	Resy	7	6	6	4
Early	Tomensa	7	4	5	5
	Karlena	6	3	4	6
	Marabel	5	3	4	6
	Erntestolz	4	2	3	4
Second	Bintje	3	3	2	3
Late	Irene	7	4	4	4
	Cara	6	5	4	5
	Maxilla	4	5	5	5
Late	Robijn	8	6	2	-

The differences result mainly from distinctions of the applied methods, which are explained later (4.1.10., 4.2., 4.3., and 4.4.). Differentials (r, R1 – R11) additional should be tested in each field test, in detached leaflet tests one times and before other tests to know the acting virulence gene combination of used isolate(s). Such differentials first of all were introduced in field growing by Schick and Lehmann (1936). In a European Concerted Action, the project EUCABLIGHT, recommended protocols for diverse tests of foliage and tubers are given as current compromise of European participants (www.eucablight.org).

The current methodical trend replaces more and more personal experience by objective results from machines, for instance in lesion estimation on leaves or in tuber tissue as applied by Douches et al. (2002b). Often such results are cheaply possible, but are of inferior value, if sufficient experience in details of blight assessment is present.

Each method has its advantage and its limits. Important questions are: Does the method consider the main aspects and factors, which influence the disease level in potato growing? If not, is another method additionally necessary and in which chronological order or has the used method to be replaced? Does the method enough bear in mind the physiological stage of the host and important environmental conditions for infection and disease progress in potato growing? High reproducibility of the result in repeated assessment is desired. However, the more a method represents complex conditions and factors of field incidence the more expenditure is necessary and the more difficult becomes differentiation of the material assessed. True polygenic quantitative resistance is most difficult to subdivide in different groups. Success in breeding requires assessment of resistance considering the most important factors influencing the resistance behaviour in the field directly and by interactions. Selection is to decide according to results of several years' average (Malcolmson1969a, Darsow et al. 1988). Examples for the frequency of wrong decisions in selection on one year's result are given by Darsow (1987a).

The intended area of growing of assessed potato material is important because of climatic conditions (distribution of precipitation, etc.) and its interaction with resistance (day length etc.). Moreover, different climates allow different levels of resistance for successful growing and therefore different methodical conditions in assessment (sub-tropics or temperate climate). In the following an overview is given about described methods including some remarks concerning application in breeding or limiting aspects.

4.1.1. Selection *in vitro*

Several methods are known and here mentioned: selection of potato plants grown *in vitro* and inoculated with *P. infestans* or selection of potato cell suspension or calli with culture filtrate of the pathogen.

An assessment of plants, cultured *in vitro*, and inoculated with *P. infestans*, is carefully possible for quantitative foliage blight resistance too as very rough pre-selection (Tegera & Meulemans 1985, Goetz 1991a, Darsow et al., 1994). This method is only usefully for wild material (sources of resistance) or other with high genetic variance of resistance, cultured *in vitro* often for other reason (fig. 10). Selection of cultivated *Solanum* species for resistance based on this method is not recommended except for hypersensitivity (Tegera & Meulemans 1985). For testing of transgenic plants the *in vitro* test was not reliable (Hoekstra 2009). Plant age, day length and the used medium influence the result. Huang et al. (2005) detected the method again and confirmed its value for assessment of hypersensitivity.

Selection on potato cell suspension or calli has been tried with culture filtrate of the pathogen instead of spore suspension (Behnke 1980, Foroughi-Wehr & Stolle 1985, Barna et al. 1993). Plants regenerated from calli resistant to culture filtrate exhibited lower susceptibility to *P. infestans* than parental plants in laboratory and greenhouse tests (Behnke 1980, Wenzel et al. 1987). However, the *in vitro* response did not match their field resistance (Stolle & Schoeber

1985, Wenzel & Foroughi-Wehr 1990). Also selection of cell suspension with culture filtrate did not demonstrate the usefulness for selection on foliage blight resistance (Cerato et al. 1993). The frequency of relative resistant variants did not differ from that caused by somaclonal variation.

In vitro mutagenesis combined with somaclonal variation is tried to exploit as method to produce suitable variation in *Solanum tuberosum* for late blight resistance (Kowalski & Cassells 1995). Practical application in breeding was not reached.

The electrolyte leakage assay used six leaf disks per clone placed in 20 ml of 15% culture filtrate of a liquid culture of *P. infestans*; conductance of the solution is measured at one hour intervals with a conductivity meter compared to control (Cristinzio & Testa 1999).

4.1.2. Seedlings selection

This method was commonly in early eliminating of progeny part without desired R-genes (Mueller 1925, Schmidt 1933, Schick 1934, Salaman 1939, Howatt & Hodgson 1954). However for quantitative resistance ontogenic and environmental predisposition cause deviating reaction (see table 3). The method considers mainly the resistance to infection (Dorozhkin et al. 1972). The inoculation access period was limited by Umaerus (1970) to 15 hours by rapidly drying the plants. Only seedlings with high susceptibility to infection are infected when they were inoculated uniformly with not to high dosage. It is applied in Sweden (Umaerus 1969a), in prebreeding at Gross Luesewitz since 1967, in Columbia since 1969 (Thurston 1971), in cultivar breeding by Sarvari perhaps 1965-1991, in SCRI Dundee since 1977 (Stewart et al. 1983a), in Finland (Kankila et al. 1995). Only few correlations are reported for the relation between seedlings and later propagation stages in the field (table 12). The own data represent calculation over all single individuals separate within each population, field assessment means specially growing with inoculation and correction because of maturity differences (Darsow 1989b). Calgari et al. (1984) calculated the correlation over the average of each of seven categories of seedlings blight attack and the average of their foliage blight attack (score 1-9) at 30 August in field assessment of foliage late blight "resistance". Their correlation is an example outside of good scientific practice.

Table 12 Correlation between seedlings foliage blight and its quantitative foliage blight resistance in following years in the field assessment.

Methods of assessment	References	Coefficient
Seedling: field assessment, plots 3 plants, 28 populations	Darsow & Oertel 1986	0.71
Seedling: natural field attack as single hill, 11 populations	Darsow, 1992b, not published	0.44-0.79
Seedling: field assessment, plots 4 plants, 11 populations	Darsow, 1992b, not published	0.26-0.76
Seedling: field assessment, plots 2 plants, 8 populations	Caligari et al. 1984	0.95
Seedling: field assessment	Stewart et al. 1983a	0.44-0.83
Seedling: field assessment	Annual Report CIP 1989	0.58

Six to eight weeks old seedlings are particularly suitable for this method (Guzman-N. 1964, Stewart et al. 1983c, Caligari et al. 1984, Stewart & Solomon-Blackburn 2004). However, plants six weeks and elder, planted on a distance of about three cm, are more than 30 cm long because of covering with foil for one day after inoculation, and progress in tuberization. Such plants are too difficult to handle in large-scale breeding. Only for research or for estimation of heredity of cross parents (Malcolmson 1976/77, Bradshaw et al. 1995b) such progeny test in a late stage is appropriate, if the whole material will be discarded after recording. Application in practical

breeding for direct selection of potential cross parents requires inoculation in an earlier stage. However, earlier inoculation got not reliable estimate of adult plant resistance according to Malcolmson (1980). A stage of 4-6 leaves after cotyledons is recommended in pre-breeding by Umaerus (1969a), Oertel (1972), Garcia et al. (1977), Darsow & Oertel (1986), Darsow (1992b). The inoculum density depends from resistance level of potato material, its stage of growing and environmental conditions including day length; between 3 x 10^3 zoospores/ml (Garcia et al. 1977, Hooker 1982), 5 x 10^4 zoospores/ml (Umaerus 1969a, Stewart et al. 1983b) and 3 x 10^5 zoospores/ml (Darsow 1992b) are sprayed to run-off. First 15-24 hours nearly 100% relative humidity is applied, but the inoculum is thereafter quickly dried (Umaerus 1969a). Temperature of 15-18°C (Stewart et al. 1983c) to 20/14°C (Umaerus 1969a) is intended, but deviations from this range are sometimes without fail.

Selection starts 4-5 days after inoculation. Severity of foliage blight of each plant is scored and summarised to a resistance level for each family (Stewart & Solomon-Blackburn 2004). In breeding practice not only seedlings without blight are carried on. Plants with symptoms may survive, if infected plant parts are cut off and fungicides are applied on day of potting and 3-5 days later. Only plants with necroses on stem ground will not survive. This method is not recommended for cultivar breeding using quantitative blight resistance (Yashina et al. 1981, Hooker 1982, Maris 1988, Darsow 1992b, Singh et al. 1997, Yashina and Simakov 2000).

Some authors applied the seedlings test without positive effect. Yashina and Simakov (2000) found no advantage in comparison of inoculated and not inoculated parts of populations. The same result was reported for CIP, Lima, Peru (Hooker 1982, Anonymous 1983). Probably the genetic variability of resistance in the used material was too low and/or the seedlings to young or under insufficient light conditions. An example for a susceptible and for a quantitatively resistant population is given in figure 11.

Unintentional progress of late blight after potting the seedlings, partly from delayed symptom expression, but mainly resulting from not avoided next infection cycle, enabled by watering the seedlings, is a real problem and a frightened experience of a beginner. In selection for hypersensitivity Mueller (1931) expected losses of 0.5% of remained plants; in compatible interaction 5-10% are hardly avoidable.

4.1.3. Whole-plant test in greenhouse

Cultivation under partly controlled conditions in greenhouse is conducted with whole plants to reduce the number of plants necessary (compared to the field) and to guarantee sufficient disease level (Guzman-N. 1964, Filippov & Ivanchenko 1964, Malcolmson 1976, Gergely 2000). Leaves remain on the plant; high air moisture is given at the beginning to support infection and again for a period of sporulation. Plant age, plant distance, temperature and date of observation influence the result. It is described as monocyclic test of few single-stem plants in stage before flowering (Saunders 1967/68), or of flower bud or flower with inoculation by spraying (Guzman-N. 1964, Main & Gallegly 1964, Malcolmson 1976, Stewart et al. 1983a, Dorrance & Inglis 1997, Gergely 2000, Stewart & Solomon-Blackburn 2004, Andreu et al. 2010). Sometimes 4-5 weeks old rooted stem cuttings are used (Douches et al. 2001). Alternatively the plants can be inoculated by dropping (Colon et al. 1995b). Warren et al. (1971) dropped on the upper surface of the leaves with a needle spore suspension 1. into a cellulose dome, attached to the leaf with lanolin or 2. on a 5 mm filter-paper disk. Inoculated plants are given in a mist chamber (near 100% RH) for 6-10 hours (Main & Gallegly 1964) to two days (Dorrance & Inglis 1997) at 15-17°C (Guzman-N. 1964, Umaerus 1969b, Stewart et al. 1983a, Colon et al. 1995b). Technical development enables very exactly controlled conditions (Butler et al. 1995). Inoculum density of 2 x 10^3 sporangia (Andreu et al. 2010) or 8 x 10^3 (Dorrance & Inglis 1997) to 15 x 10^3 per ml (Colon et al. 2004a in www.eucablight.org) were used, Saunders (1967/68) inoculated 25 x 10^3 zoospores per ml.

The level of late blight is rated 6-8 days after inoculation as score (Stewart & Solmon-Blackburn 2004, Oosumi et al. 2009) or % blighted foliage area (Douches et al. 2002b); symptoms similar to hypersensitivity are additionally recorded. In different manner the result is calculated from the course of disease. Main and Gallegly (1964) tested six weeks old plants grown from eye buds after spraying with suspension and controlled incubation. Repeated readings after 5-20 days over 3x25 plants per clone were summarized over frequency in groups of disease level to an index. Wild and cultivated potato material is assessed on rooted cuttings from true-seed germplasm by spraying of 4-5 weeks old plants with a mycelial/sporangia suspension of one isolate of unknown virulence (Douches et al. 2001); the percentage of diseased stem and leaf area is estimated one and two weeks after inoculation. Malcolmson (1976) considered lesion number and lesion size on leaves, petioles and stems seven days after inoculation and summarised that this test gives a good forecast of field performance. Results of field assessment and greenhouse correlated with r = 0.62 to 0.78 (Stewart & Wastie 1982). In UK new cultivars have been finished assessment of six replications of one 42 to 49 days old plant sprayed with 10^3 sporangia ml^{-1} to be accepted on the National List. The percent plant area affected is recorded after six days; cultivar means are adjusted for year differences (Carnegie & Cameron 2001). Andreu et al. (2010) recorded blight severity (%) daily from 4-11 days after inoculation and calculated rAUDPC, which then were transformed to a 1-9 scale with Shepody as susceptible standard fixed 8.

Additionally components of resistance are assessed as infection efficiency (number of lesions per area), lesion growth rate (daily measure of lesions), generation time (interval between inoculation and new sporulation) is sometimes named latency period (Singh & Birhman 1994) and sporulation capacity by counting of sporangia per area on one date or over time. Details are considered below (4.1.11.). Porter et al. (2004) inoculated leaflets, stems and young flowers with soaked filter paper discs. The plants were then placed in a mist chamber for 18 hours followed by a 24-hours dry period and replacing in a greenhouse; lesion size (width and length) was measured on leaflets, stems and flower pedicles every 12 hours and the area under the lesion expansion curve (AULEC) was calculated for each leaflet, stem and flower. The end point of measuring was 1. when the leaflet lesions of the most susceptible clone reached 100% of the leaflet area, 2. when stem and flower lesions expanded down one half of the stem or pedicle. The sporulation capacity was assessed on plants which were removed from greenhouse five days after inoculation again in a mist chamber for 18 hours; then 12-mm-diameter section were taken by means of a cork borer from leaflets that half of the bore diameter extended into healthy-appearing tissue and the other half into the lesion. Weihing and O'Keefe (1962) determined sporulation on leaves after spraying of suspension on single leaves on whole plants and progress of mycelium in single leaflets after dipping in suspension, both over a period of several days. Miller et al. (1998) compared 22 isolates by assessing components of resistance.

Whole plant test in greenhouse resulted best correlation with resistance behaviour in the field according to Hoekstra (2009).

4.1.4. Whole-plant test in the field

Pietkiewicz (1978b) calculated rate of infection (r according to van der Plank 1963), delay of appearance of foliage blight symptoms compared with the most susceptible cultivar and duration of three epidemic stages (logarithmic, intermediate and last stage) in days from detailed field observations. The lack of interaction cultivars x years enabled analysis of three year's average of 26 cultivars in five maturity groups. Only mid-late and late varieties showed different rates of infection within its maturity group. Second early, second late and late cultivars differed within the maturity group concerning delay of epidemic onset.

Colon et al. (1995a) assessed single plants in detail in field conditions too, planted at a distance of 0.75 x 0.40 m. Lesion growth rate, generation time and sporulation capacity were estimated.

The described methods seem not suitable to be applied in breeding practice.

4.1.5. Combined field-laboratory tests

Dorozhkin at al. (1972) developed and applied a method, in which leaves are inoculated in the field by dropping in the evening. The drop is covered 12 hours by a micro-chamber; 15 inoculated leaflets are cut off after three days and incubated in laboratory under usual conditions. Eight days after inoculation lesion size is measured (mm) and intensity of sporulation is scored. Incubation time is recorded in days and is used as denominator to calculate an index with the product of lesion size in mm x sporulation score 1-3 as numerator (Dorozhkin et al. 1972). This test method considers very well predisposition in the most critical part of pathogenesis with sure results in average of six dates of inoculation per year.

Colon et al. (1995a) measured lesion growth rate in the field; and after final measurement detached leaflets were placed 24 hours in moist chamber to count number of sporangia.

4.1.6. Detached leaflets test

Exact comparison of detached leaves with such remaining on the plant showed higher defence level on the whole plant (Vinogradova 1940, Warren et al. 1971). Dorozhkin et al. (1972) stated better differentiation of clones tested in the variant of not detached leaflets. The crucial question considers the interaction cultivar/method, which seems not to be important (Vowinckel 1926, Huettenbach 1951, Haussdoerfer 1959a, Malcolmson 1969a), although symptoms on greenhouse-grown leaves may differ from that of field-grown plants of the same variety (Huettenbach 1951). The effect of detaching seems to be smallest during potato flowering (Lowings & Acha 1959) and did not affect sporulation in comparison with whole plants in experiments of Harrison and Lowe (1989). Detached leaves are not only used for assessment of resistance but also for testing of aggressiveness of isolates (Miller et al. 1998).

Carlisle et al. (2002) cut the leaflets from 6-8-week-old-test plants. The time of the day, in which the leaflets are detached, influences the result of assessment. Leaves detached at five o'clock were most susceptible; such from 17 o'clock were least susceptible (Haussdoerfer 1959a). Umaerus and Lihnell (1976) took samples of 20 not terminal leaflets in the morning. Inoculation a day after detaching resulted in increased resistance (Schaper 1951). Using of detached leaves (Vowinckel 1926) or leaflets (Haussdoerfer 1959a, b, Malcolmson 1969a, Umaerus & Lihnell 1976, Nilsson 1981, Bobkova et al. 1982, Tooley 1990, Swiezynski et al. 1991, Colon et al. 1995a, Zarzycka 2001a) from the first two full expanded leaves of the plants from the top grown in greenhouse or field has logistic advantages and independence from weather conditions outside during the test. This test method was earlier commonly applied to test R-gene resistance (Toxopeus 1954, Wriedt 1955, Schick & Hopfe 1962), but gives helpful information on quantitative resistance, if some conditions are considered: testing of plants of nearly the same physiological stage (maturity); cut leaflets of determined position (Stelzner & Lehmann 1944, Visker et al. 2003a); adapt inoculum density to potato material tested (Yashina & Erochina 1977), appropriate plant stage and environmental conditions. Assessment more at the end of flowering gives more reliable (stronger) estimation (Haussdoerfer 1959a, own experience). The detached leaflet assay is suitable for assessment of breeding material or isolates in large scale (fig. 12).

Inoculation of leaves by dipping in spore suspension is applied by Schaper (1951) and van der Zaag (1959). Drop-inoculation (one or two drops of 10 or 40 µl) on the underside dominates and is suitable for most assessment aspects, but for testing of infection efficiency spraying is to prefer (Haussdoerfer 1959a, Lapwood 1961c, Umaerus & Lihnell 1976, Nilsson 1981, Bobkova et al. 1982). Some authors fix the drop by using a soaked filter paper disc (Knutson 1962, Porter et al. 2004, Inglish et al. 2007). In the field about 80% of infections happen via the upper side and stomata (Bjoerling & Sellgren 1955, cited by Umaerus 1963). Inoculation of the upper side is half to a sixth as effectively as the underside. Lesser number of stomata, slower disease progress and partly higher dropping down of inoculum cause more variable results (Umaerus 1969a). However, differences between potato clones were greater when the upper leaf surface was

inoculated (Umaerus 1970). Pietkiewicz (1977) found r = 0.41, 0.80, and 0.94 between inoculation of upper to underside for percentage of not blighted leaflets, resistance to penetration and resistance to spread, respectively. Malcolmson (1969a) compared inoculation of leaflets by dipping in suspension, by inoculation with filter paper discs dipped in spore suspension, and spraying of inoculum. Inoculum density of 2.5×10^3 to 5×10^4 sporangia/ml is applied. Usually the leaflets are turned over after about 20 hours; several authors actively remove the inoculum drop.

Different variants of moist chamber support very high air humidity to keep the inoculum drop for at least six hours, better 15 hours (Umaerus & Lihnell 1976) or 16 hours (Bobkova et al. 1982) to hold the leaflets turgescent, and to conduct sporulation from the fourth day on. Bobkova et al. (1982) finished the infection period after 16 hours by drying the leaflets. Harrison et al. (1994) realized first six hours 100% air humidity, then 18 hours 45% to dry the inoculum drops and inhibit bacterial attack; petiole of leaflets were dipped in distilled water. Instead of distilled water Inglish et al. (2007) placed petioles with three terminal leaflets in a sucrose nutrient solution in test tubes; after inoculation the chamber was misted for one minute every 20 minutes.

The preferred temperature of incubation is chosen near 16°C (Zarzycka 2001a, Colon et al. 2004b in www.eucablight.org). Guzman-N. (1964) incubated first 18 hours at 15°C. Wriedt (1955) mentioned problems by bacterial rotting of leaflets or its becoming glassy without sporulation. Different conditions of light were applied: permanent light (Vowinckel 1926, Nilsson 1981, Zarzycka 2001a) or most frequently 16 hours light with different quality and intensity (Flier 2001); Rubio-Covarrubias et al. (2006) used 12 hours light at 18°C, Porter et al. (2004) 18 hours at 15°C. Oosumi et al. (2009) applied first 24 hours darkness, then six hours photoperiod with $400 Em^{-2} s^{-1}$.

A wide range of number of leaflets per test and of replications is described, depending from aim, available potato material, personal and room. Seven leaflets or six pairs of leaflets per clone were considered sufficiently (Tetowski & Piotrowski 1975). Observation of the leaflets is conducted one times after 5-6 days (Mooi 1966, Zarzycka 2001a), two different days (Haussdoerfer 1959b, Darsow et al. 1988) or on several successive days (Warren et al. 1971, Dorrance and Inglish 1997). Standards in each maturity group and differentials (r, R1–R11 and more) should be involved to check virulence and aggressiveness and enable comparison of different tests.

Test of detached leaflets is more used to assess single components of resistance than quantitative over-all resistance (Miller et al. 1998, Hoekstra 2009). If the last is intended, lesion growth and sporangia production per area are mainly considered (Vowinckel 1926, Schaper 1951, Kaiser & Klinger 1955, Haussdoerfer 1959a, b, Umaerus 1963, Weindlmayr 1962) by visual scoring (Zarzycka 2001a) or measuring/counting, respectively. Dorrance and Inglish (1997) considered only percent of colonized leaflets and lesion size (% of the leaf area). Oosumi et al. (2009) used the lesion diameter by applying a computer-driven image analysis system. Calculation of an index from tested components is proposed by Mueller and Haigh (1953), Lapwood (1961a), Popkova and Bychenkova (1968), Filippov et al. (1986). For instance Filippov et al. (1986) considered the number of necroses per 1 cm^2 three days after spray-inoculation, the diameter of necroses 75-80 hours after drop-inoculation, the number of sporangia from 10 leaflets, and incubation period. One to several dates of observation is used. Popkova and Bychenkova (1968) calculated the product of score for sporulation intensity x lesion diameter in mm four and six days after inoculation and divided the sum of both by duration of the incubation period in days. Singh and Birhman (1994) estimated resistance components by testing detached leaflets (AUDPC = 0.1082 + [0.0178 x lesion size] + 0.0045 x total sporangia number). The equation accounts for 82% of variation in field assessment. Yang et al. (2007) consider the method suitable for high-throughput investigation. Miller et al. (1998) calculated the area under the lesion expansion curve (AULEC). Yashina and Erochina (1977) stated a correlation between results from detached leaf test and field assessment of r=0.765.

Unexpected high variability between different test dates and between the leaflets in a test for some potato clones is remarked by Lapwood (1961a), Harrison et al. (1994) and Dorrance and Inglish (1997), despite high standardization level. Tegera and Fouarge (1984) concluded that the detached leaflet test is too stern to identify moderately resistant and moderately susceptible groups of potato clones, whereas Zarzycka (2001a) found "this method does not permit differentiation and ranking of more resistant potato genotypes." Malcolmson (1969a) concluded that assessing detached leaflets with inoculation of the underside in general agreed with those from whole plants grown in greenhouse or field, but higher levels of resistance were recorded as more susceptible. Young et al. (2007) observed little correlation between competitive fitness of isolates in the field and their aggressiveness on detached leaflets. Similar Haynes et al. (2007b) found lesion size on detached leaves correlated r = 0.18-0.24 with field evaluation as AUDPC. Only little correlation was found between competitive fitness of isolate mix in the field and its observed aggressiveness on detached leaflets in the North Ireland study (Young et. al. 2007).

Tests between mid of July and end of August are not recommended, mainly from greenhouses, because of high environmental stress of tested plants (Toxopeus 1954, Haussdoerfer 1959a). Leaves from eye cuttings can be more susceptible than such from plants grown from whole tubers of the same cultivar (Schaper 1951) due to different physiological stages. A distinct influence of maturity stated Haussdoerfer (1959a). Late varieties showed after 4-6 days one third of the sporulation intensity of early ones. He empirically adjusted the calculated index of incidence to maturity and enabled that way comparison of clones independently from its maturity (table 13).

Table 13 Table for transformation of index of incidence of leaflets to the level of resistance according to Haussdoerfer (1959a). Average of 3 x 6 leaflets per clone tested.

Maturity	Resistance	Intensity of sporulation		Index	Level of resistance
		day 4 (x1)	day 6 (x2)	2(x1) + x2	(fixed score)
Early	low	4	4	12	1.20
	middle	3	4	10	1.00
	high	2	4	08	0.80
Second early	low	3	4	10	1.25
	middle	2	4	08	1.00
	high	2	3	07	0.88
Second late	low	2	4	08	1.33
	middle	1	4	06	1.00
	high	1	3	05	0.83
Late	low	2	3	07	1.40
	middle	1	3	05	1.00
	high	0	3	03	0.60

4.1.7. Leaf-disk test

The leaf disk test is today mainly applied in assessment of fungicide effects, fungicide resistance or in research. Disks of 1.5 cm diameter cut with a cork-borer from 1-2 of the youngest full developed leaves two month after planting are inoculated on the upper side with a drop of 0.045 ml suspension (Hodgson 1961), 0.010 ml (Flier and Turkensteen 1999) or sprayed with zoospore suspension (Mueller 1953, Mueller & Haigh 1953). Three plants per clone were used with 20 disks each and inoculated with 200 zoospores per drop (Hodgson 1961). Percentage of sporulating disks is recorded after one week. Hodgson (1962) showed differences in resistance components on selected cultivars by reading on several dates and considering percentage attacked disks (penetration), mycelial growth (size of lesion) and intensity of sporulation. Mueller & Haigh (1953) comprised infection efficiency and sporulation intensity, assessed in the lab, and late blight generation number in the field in an index. Hodgson (1962) and Ullrich and Krug (1965) calculated an index from different classes of sporulation intensity and its percentage of disks.

Flier and Turkensteen (1999) placed the disks in plates (Greiner no. 638102) on water agar, inoculated with 2 x 10^4 sporangia/ml and incubated the plates in plastic trays enclosed in a transparent polythen bag at 15°C first 15 hours in dark, then in 16 hours photoperiod. Readings started 72 hours after inoculation with intervals of 12 hours to estimate the latent period. The fraction of sporulating disks was calculated, and sporulation was stated in suspension by means of a Coulter counter. The "latent period" was calculated in hours to reach 10% of the total sporulating disks, the speed to reach the maximal number of blighted disks, the sporulating intensity as natural logarithm of the average number of sporangia per cm^2. The infection efficiency index was derived from sporulating disks after eight days. Because authors were focussed on pathogenicity instead of a resistance index a composite aggressiveness index was calculated by multiplication of latent period with speed of appearance of sporulating lesions, infection efficiency and spore number. In breeding practice this tests could not be established.

4.1.8. Stem assay

Lapwood (1961c) analysed stem and petiole infection from inoculation of 10 leaf axils per stem. The number of blighted petioles and blighted stems was counted one and two weeks after inoculation followed by 24 hours moist chamber. Stem cuttings from field or greenhouse, 10-20 cm long and free of fungicide application of plants in stage of flowering may be maintained in tubes or glasses with water or nutrient solution and are inoculated by filter paper squares soaked in spore suspension of 1.7 x 10^4 sporangia/ml. Dorrance and Inglish (1997) placed the inoculum 3-5 cm below the top of the stem cutting and incubated the stems in a growth chamber at 20°C with 12 hours light for seven days. Lesion length was measured. Significant cultivar differences are found.

Pietkiewicz (1976) cut a 5 cm long stem piece from the middle part, inoculated by spraying and calculated percentage of infested pieces. Kapsa (2002b) changed the method by dropping the inoculum and measured the length with discolouration. In assessment of gene bank material lesion growth rate is used in stem assay (Hoekstra 2009). Lammers et al. (1998) cut six about fife cm long internodal parts from one stem per plant, 10 plants per clone; the stem sections were drop-inoculated and in moist chamber incubated at 15°C with a day length of 16 hours for 9 days. The results were compared with spray-inoculated field-grown plants and showed that stem sections lying in the lab do not react as stems on intact plants. Cultivar-specific details of the stem architecture, which influence the duration of drops and possibility of infection, are not considered in simple tests of lying stem sections. Resistance of leaves did not correlate to resistance of stems in field experiments, which underlines necessary attention to both parts of haulm resistance in resistance breeding. Incidence of leaves and stems correlated r = 0.56 – 0.75 in experiments of Kapsa (2002b). At ZL Gross Luesewitz both parts are considered in field assessment since long time.

Perhaps a field assessment with double setting of potato seed tubers according to Keil et al. (2010) is a suitable method of stem assay, in which a healthy tuber is planted adjacent to an inoculated one. This method gives relative high percentage of early stem infections, but is not used for screening of potato collections up till now.

Already Vowinckel (1926) assessed speed of mycelial spread in leave stalks of different clones. Application of stem assay for testing of hypersensitivity is mentioned by Hoekstra (2009). Few cm long potato sprouts are tested by Liu and Weber (1997).

4.1.9. Assessment of foliage blight resistance using ELISA or PCR

Resistance to colonisation (spread of *P. infestans* in potato tissue measured as lesion growth rate) may be assessed by ELISA (Harrison & Perry 1990, Harrison et al. 1990, Knapova 1995). If the methodical development is finished, it should be advantageous for assessment of resistance to spread of the pathogen.

A quantitative PCR has been developed to assess the growth of *P. infestans* in resistant and susceptible tomato (Judelson & Tooley 2000), which is very highly sensitive and could be applied for the in planta quantification of pathogen biomass (Kamoun & Smart 2005).

4.1.10. Field assessment of foliage blight resistance

Assessment in the field has the highest risk to be ineffective because depending from whether course on the one hand, however, may be the most reliable method because all environmental and ontogenic factors, which are effective in growing practice, take part in the resistance reaction, on the other hand. Therefore Russel (1978) recommended: "Wherever possible, screening and selection tests for resistance to fungal diseases should be carried out in the field." This method requires adequate design of the test material in growing, guaranteed compatible host-pathogen interaction and regulation of leaf wetness duration.

Field tests can be classified into such without inoculation (Niederhauser 1972, Birhman & Singh 1995, Trognitz et al. 2000, Dorrance et al. 2001, Gopal & Singh 2003/04, Mulema et al. 2004/05, Porter et al. 2004, Ellissèche et al. 2005, Rivera-Pena 2005, Andrivon et al. 2006, Rahkonen et al. 2006,) and with inoculation (Erjefaelt 1975, Malcolmson 1976, Hooker 1982, Caligari et al. 1985, Beekman 1987, Darsow 1989a, Chatot et al. 1995, Colon 1994, Platt & Tai 1998, Chatot & Bersihand 2004, Douches et al. 2004, Stewart & Solomon-Blackburn 2004, Zlesak & Thill 2004, Mollov & Bradeen 2007). Main argument against inoculation is the risk to introduce increased pathogenicity to the own location (breeding garden). However, the small chance to utilize quantitative and polygenic blight resistance successfully requires avoiding of each methodical deficiency. Kessel et al. (2006) inoculated the spreader rows with a mixture of 15 current isolates. Cooke et al. (2001) inoculated two leaves only of every fourth plant within the spreader rows. Clayton & Shattock (1995) inoculated at weekly intervals by attaching three heavy-sporulating leaflets with string to the petiole of a terminal leaflet of one middle leaf on one central plant of each plot. Spraying of suspension is usually, frequently on spreader rows; inoculation by repeated transferring sporulating potato plants from greenhouse into the plots is another method (Malcolmson 1976, Stewart et al. 1994). Inoculation of all plants often resulted in quick disease progress with lesser differentiation. Inoculation through the field irrigation system as applied by Douches et al. (2004) is labour-saving, but perhaps not evenly enough. Mollov and Bradeen (2007) showed that design with spreader rows has no advantage compared with direct inoculation. Inoculation before flowering brings slower disease progress than inoculation at the end of flowering (own experience). Field assessment trails which rely on natural inoculum in common trail design are usually not adequate because they accept wrong results from R-gene effects as described by Griffin et al. (2010); score 8 was given for Setanta instead of 3.

Supporting of disease progress by irrigation (Rotem et al. 1970, Fry 1975) and reduction of

wind should be arranged (Darsow 2003a, see 4.2.3.). Mulema et al. (2004/05) separated each 60-plants potato plot by intercropping with one-meter wide barley strips to minimize interplot interference. Bobkova et al. (1982) isolated the 15 m^2 plots by surrounding with cereals.

Simple field observation is suitable only in regions as Toluca valley (Niederhauser 1962, Lapwood 1971, Rivera-Pena 1995, Lozoya-Saldaña 1999, 2002, Novy et al. 2007) and parts of peninsula Sakhalin at Far East of Russia (Loktina 1969, Elansky et al. 2001); except the material is free of R-genes. However, equally occurrence of all virulence genes seems not to be realized, even at the Toluca valley; race-genotype interaction is limited but consistent. Differentials R9, R5 and R2 were the last ones with late blight symptoms and slower progress (Belmar-Díaz et al. 2009). It is unknown, if these differentials quantitative resistance, lateness or plant habit delay the development or factors of the pathogen. Outside of these locations inoculation with highest qualitative and quantitative pathogenicity is required.

To reach similar physiological stage of all maturity groups at one date of inoculation is proposed to plant according to maturity group at different dates (Young & Young 1958). It is easier to plant the test clones on the same date, but of the same maturity group neighbouring to each other (Stewart & Solomon-Blackburn 2004) and - if known - resistant and highly susceptible clones not random mixed (Darsow 2003a). The deviation of the resistance level by spore influx from the neighbour clone was stated near a halve score (Conolly et al. 1995), but it depends from plot size, method of inoculation and other, and can be more than two scores (Darsow 1989b). In no case border rows are allowed to save; they tend to be too low infested against main wind direction. The spreader rows do not cause a constant efflux to more than one neighbour row (Turkensteen 1973).

Plot size and replication number are important and often not enough appropriated to quantitative nature of host-pathogen interaction (van der Plank 1963, James et al. 1973, 1976, Paysor & Fry 1983, Parlevliet 1993). One plant (Stewart et al. 1994, Bisgonin et al. 2002), two plants (Bradshaw et al. 1995b) to 72 plants per plot (Singh & Birhman 1994) are usually grown, without or with replications, for instance two replications with two plants (Bradshaw et al. 1999, Stewart & Solomon-Blackburn 2004) or with six plants (Chatot et al. 1995), three replications with one plant (Stewart et al. 1994), four replications with 10 plants (Erjefaelt 1975, Platt & Tai 1998) or four with five rows of ten plants each (Singh & Bhattacharyya 1995). In case of locally very limited inoculation (point-source inoculation) one replication may be sufficient (Darsow 2003a). The larger the plot, the more *P. infestans* cycles of propagation occur mainly within the plot, and are polycyclic mainly influenced by the own sporulation intensity. Kirk et al. (2000) used point-source inoculation in assessment of fungicides.

Erjefaelt (1975) expressed the resistance level as days between first symptoms in inoculated spreader rows of Majestic and 50% defoliation of each test plot. Commonly disease level is estimated in a 1-9 scale (Darsow 1989b, Chatot et al. 1995, Stewart & Solomon-Blackburn 2004), a 1-5 scale (Gopal and Singh 2003/04) or as percentage (Beekman 1987, Forbes & Korva 1994, Singh & Birhman 1994). The number of observations in a season varies from one (Hodgson 1962), or two (Beekman 1987) to 19 (Darsow 2008), often weekly intervals are preferred. Different procedures of calculation the resistance level are known as calculation of an index (Guzman-N. 1964, Platt & Tai 1998), a weighted sum of the three most representative consecutive assessments (Chatot et al. 1995), area under the disease progress curve, AUDPC (Shaner & Finney 1977, Colon 1994, Clayton & Shattock 1995), relative AUDPC (rAUDPC, Fry 1978, Flores-Gutierrez & Cadena-Hinojosa 1996, Platt and Tai 1998, Hansen et al. 2006b, www.eucablight.org) or days after planting to reach the 5% level of foliage blight (Dorrance et al. 2001). Although the influence of lateness can a little be reduced by rAUDPC, Darsow and Hansen (2004) showed a correlation coefficient between rAUDPC and maturity of $r = 0.72$ in opposite to the empirical method (Darsow 1989b) for calculation of foliage resistance with $r = -0.18$ to maturity (see table 17). An adjustment to reference cultivars was conducted empirical by selec-

tion of suitable section of the DPC according to maturity (Darsow 1989b). In majority of the methods mixed effect of maturity and resistance is applied as 'resistance'. Chatot and Bersihand (2004) estimated the score of resistance by the weighted mean of three consecutive scores and chose the best date-combination from results of standard cultivars and R-gene differentials. A transformation to percentage of necrotic tissue is used for calculation of rAUDPC. Hansen et al. (2005) made results of different years and location better comparable by expressing it relative to an included standard. Is one standard sufficient because of interaction clone-year? The 1-9 scale values were estimated using parameters derived with following linear regression model: $y = a + b(x)$ where y = observed scale values; a = intercept; b = slope parameter; and x = (√rAUDPC of tested clone/√rAUDPC of standard Oleva) x 100. Standard Oleva was given score 4, Berber score 1 (very susceptible) and Kuras score 8 in the model (Hansen et al. 2005). Dose-response curves were developed by Kroll and Eide (1981) after spraying with a series of inoculum densities related to primary infections. The cultivars differed in slope of regression line of disease.

There is a wide range how many dates of observation are necessary. For rough grading of germplasm accessions Gopal and Singh (2003/04) regarded scoring at a single appropriate date (dependent from susceptible standards) for two years in a non-replicated trail as sufficiently in the conditions of Shimla. The AUDPC-values correlated with scoring 1-5 in two years average r = 0.85-0.9, with scoring 1-9 r = 0.92-0.95. Tazelaar (1981) preferred weighted mean method for characterization of gene bank material. Grading on scale 1-9 is recommended for breeding purpose. At least two years were more important than replications. Stewart & Solomon-Blackburn (2004) pick afterwards the weekly evaluation the date that gives the best discrimination between control cultivars for characterization of resistance. According to Beekman (1987) two dates of observation are sufficient for assessment of cultivars growing with two replications of six plants each. Truberg et al. (2010) consider three ratings as sufficiently instead of ≥ 16 from statistical point of view on conditions of Gross Luesewitz if the quality of visual estimation remains the same. However, that is not expected. Moreover, other causes of dying (maturity, *Alternaria* sp. and other) can than not or insufficiently be separated from late blight effects.

In comparison of the methods of field assessment its application in different climates is to consider. What is sufficient for tropic highlands with lower temperature and slower disease development can be expected as not enough adapted to often explosive disease progress in temperate climate.

Frequently the estimation of foliage blight incidence considers mainly percentage of invaded leave area. However, the relation of leaves, stems and flowers may be approximately 70, 26 and 4% of the haulm mass, respectively (Porter et al. 2004).

Results of different years of assessment at Toluca valley correlated r = 0.72, 0.65 or 0.82 (Inglish et al. 2007). To the field results (rAUDPC) at Mount Vernon in USA the Mexican results correlated r = 0.53. Results of detached leaflet-test and field assessment showed correlations of r = 0.45-0.62 (Inglish et al. 2007). Assessment of quantitative resistance remains statistic information about a variable trait, in which each methodical insufficiency has to be avoided.

4.1.11. Components of quantitative foliage blight resistance

Decades ago apparent infection rate (AIR) was used as suitable characterization of disease progress recommended by van der Plank (1963). However, for some practical reasons other or additional characterization is commonly. Assessment of single components of resistance (host differences in single parts of the disease course) has the aim to select potato clones with best resistance to single components and enable combining of the components by breeding (Ross 1986). Resistance to penetration (infection efficiency), resistance to mycelial spread (size of lesion, lesion growth rate, amount of mycelium), length of latent period (interval between inoculation and development of symptoms), length of generation time (interval between inocula-

tion and begin or 50% of maximal sporangia production) and different sporulation capacity are such components probably caused by (partly) independent resistance genes (van der Zaag 1959, Hodgson 1962, Umaerus 1970, Wastie 1991, Colon 1994). Crossing or fusion of clones with different components of resistance could increase the resistance level of a part of the progeny above the level of the best parent by complementation each other (Hodgson 1962, Ross 1986). Therefore analysing these components is necessary and is examined for instance by Umaerus and Lihnell (1976). Its application first line should be realized in pre-breeding together with considering of some passive factors. In variety breeding such detailed methods rather unlikely will be employed (Hodgson 1962, Johnson & Taylor 1976). However, components of active resistance and factors affecting passively the development of foliage blight operate simultaneously with changing relations in different plant stages (Singh & Bhattacharyya 1995). Therefore the effect of single components can have varying value at the same cultivar or conflicting results (van Oijen 1992) and selection for single components should not be overestimated. Different components may be differently affected by climatic conditions (Rubio-Covarrubias et al. 2005) and ontogenic plant stage. That means one snapshot needs not to be sufficiently to explain the overall resistance behaviour (be representatively for it). So Malcolmson (1969a) did not find any clear correlation between the components tested as well as its relation to resistance rating in the field.

Resistance to infection: The term is used by us in a broad sense and means that the pathogen could not successfully establish. Waxy layer, osmotic pressure or leaf exudates may variety-specific influence zoospore encystment, germ tube growth and penetration (Pietkiewicz 1976). Resistance to infection is measured as infection efficiency (IE) and is mainly an active reaction of potato clones and in some cases supported by constitutional factors. Umaerus and Lihnell (1976) calculated IE as number of lesions per cm^2 divided by the number of spores per cm^2 inoculated, after three days. The number of penetrations increased 138% at 16°C and 16 hours light compared with incubation at 24°C during test; a significant interaction of cultivars occurred with temperature and with penetration sites (Rubio-Covarrubias et al. 2006).

This component was assumed to be very important by many authors (Mueller and Haigh 1953, Black 1954, Kaiser and Klinger 1955, Haussdoerfer 1959a, van der Zaag 1956, 1959, Hodgson 1962, Umaerus 1969b, 1970, Osipova et al. 1976, Nilsson 1981, van Oijen 1992, Colon et al. 1995b, Cañizares and Forbes 1995). On susceptible cultivar Bintje from five zoospores followed one infection and sporulating lesion; resistant hybrids required at least 60 zoospores in a drop, Ackersegen more than 100 (Umaerus 1969a, 1970). Minimal inoculum was stated eight zoospores in a drop of 0.01 ml for Bintje, 24 zoospores for Pimpernel (Lapwood 1968). Cultivar Voran required the 8fold inoculum density as Cherokee for the same disease level (Hodgson 1961). Sebago is an example for a cultivar with resistance to infection (Hodgson 1962). Mexican cultivars possess mainly resistance to infection (Lapwood 1971, Clark 1978). However, Birhman and Singh (1995) found in a study with 16 cultivars no significant correlation between IE and rAUDPC, similarly Dorrance and Inglish (1997). Main and Gallegly (1964) as well as Knutson (1962) considered this component as very variable and not suitable for selection of breeding material. Kammermann (1951) stated low correlation of IE to resistance in the field. High intragenotypic variation and higher genetic than phenotypic correlation to rAUDPC are explained by high environmental effect on IE (Birhman and Singh 1995). On the contrary, Guzman-N. (1964) and Umaerus and Lihnell (1976) found good correlation of IE to foliage resistance in the field. Colon et al. (1995b) stated the tendency of lower IE on resistant clones of some wild species, but others not. Low genotypic coefficient of variation and genetic advance as well as heritability were found for IE on wild material by Chauhan et al. (1999). Only Umaerus (1969b) mentioned that selection to low IE did not lead to selection on late maturing type, which would be expected to agree with hypersensitivity. Indeed, this component could most evident reflect the effect of inoculum dilution by active R-genes (which reduce a part of the inoculum) as well as lateness (to good results because assessment in physiological to early stage).

Negative selection on seedlings in stage of cotyledons or first leaves or several weeks old plants is mainly a selection to IE (Dorozhkin et al. 1972).

The methods to estimate IE differ. Lapwood (1961b) sprayed the upper side of eight leaves per cultivar, incubated in a moist chamber at 15°C 24 hours followed in cool greenhouse conditions up to counting of lesions per leave area on two days. Bobkova et al. (1982) sprayed a low zoospore density, limited the penetration period to 18 hours and counted the number of necroses after three days at 19-21°C in a moist chamber, Filippov et al. (1986) at 18°C. Colon et al. (1995b) expressed IE as chance p of a single spore to be successful from the fraction of inoculum drops that resulted in growing lesion using the formula $p = 1\text{-}H^{1/k}$ according to Swallow (1987), in which H = % of unsuccessful inoculations, k = number of spores in a drop. Singh and Birhman (1994) counted the number of infection points per 1000 zoospores germinated and 0.025 ml per leaflet three days after spraying on the lower leave surface with an autodispensor. Data of IE were transformed to arc sin square root. Singh and Bhattacharyya (1995) expressed IE as number of lesions divided by the estimated number of germinated zoospores. Rubio-Covarrubias et al. (2006) dropped detached leaflets abaxial with 10 µl and cut this area 48 hours later by a 6-mm-diameter disk for counting of penetration sites per disk after fixing, re-hydrating and mounting in glycerol. Other authors used the percentage of successful drops as measure of IE (Flier & Turkensteen 1999, Carlisle et al. 2002).

Cultivar Ackersegen is an example for a field-resistant clone without resistance to penetration (Guzman-N. 1964), whilst Eva and Saphir possess resistance to penetration (Osipova et al. 1976). Variety Pimpernel is an example of low IE (Lapwood 1963, Wilson & Coffey 1980), Saphir too (Osipova et al. 1976). IE was lower at 12 hours photoperiod than at 16 hours (Rubio-Covarrubias et al. 2006). Ullrich and Krug (1965) found increased IE due to reduced day length prior inoculation.

Resistance to mycelial spread was assessed by repeated measuring of lesion diameter 4-7 days after drop inoculation of single leaflets on plants in greenhouse or field, the area was calculated and its daily difference of square root as linear lesion growth rate (LGR) averaged in mm per day (Colon et al. 1995b). Only lesions were considered which reached a final size of > 5 mm^2 and a growth rate > 0.1 mm per day. Examples for hypersensitive-like reaction caused by quantitative resistance are visible in figure 13 and 14. LGR was assessed on detached leaflets and on leaves on intact plants in the field (Colon et al. 1995b). On whole plants in greenhouse and field increase in radial expansion of lesions were measured by Warren et al. (1971) four, six and ten days after inoculation and compared with detached leaves, separated for leaf position 3-18. Guzman-N. (1964) investigated the lesion size after inoculation by wad of cotton, dipped into suspension and placed in the centre of leaflet, or by hypodermic injection of suspension at the base of terminal leaflet. Lapwood (1961c) inoculated the under side of three leaflets per leave by means of a filter paper disk soaked in suspension and measured the radius of the lesions four days after inoculation. Umaerus and Lihnell (1976) measured only along the axis parallel to the main vein after drop inoculation. Bobkova et al. (1982) and Filippov et al. (1986) measured the diameter of lesions about 96 hours after dropping and incubation at 20°C; the drop was removed after 18 hours. Carlisle et al. (2002) measured the lesions on three consecutive days in parallel to the midrib and at right angle to it. The cumulative totals of the lesion areas from daily length and breadth measurements in mm^2 resulted in the area under the lesion expansion curve AULEC from 1-7 days after drop inoculation with 24 hours penetration time. Similarly Porter et al. (2004) calculated AULEC of leaflets, stems and flowers from assessment of whole plants in greenhouse. Birhman & Singh (1995) measured the lesion size once after six days calculating the lesion area = (π/4) x length x breadth and transformed the data to square root; but they inoculated the leaflets by spraying. Lesion length (a) and breadth (b) were measured three days after inoculation from greenhouse-grown leaflets by Singh and Bhattacharyya (1995); the lesion size was calculated as (π x a x b). Some cultivars develop less necrotic lesions; they sporu-

late on green leaves with delayed or without necrotization as Darjeeling Red Round (Sharma et al. 1975). Between local cultivated germplasm in Bolivia the LGR varied about six-fold (Gabriel et al 2007).

Quite different from rating disease symptoms, it is possible to state the amount of *P. infestans* in each leaflet from defined drop inoculation by plate-trapped antigen ELISA, using polyclonal antiserum. In comparison with reference samples with known mycelium content in dilutions of homogenized leaf material the mycelial amount as mg fresh weight can be estimated (Harrison et al. 1994). The results of this method are governed by environment and other factors in the same level as other.

Vowinckel (1926) found LGR a useful component of resistance. Nilsson (1981) did not find a significant correlation of five days old lesions of *S. tuberosum* subsp. *andigena* and *S. phureja* to its field resistance, while Guzman-N. (1964) recorded large differences. Knutson (1962), Main and Gallegly (1964), Gees and Hohl (1988) tested cultivars and recorded little differences; they did not recommend LGR as useful indicator of resistance in the field. Lapwood (1971) and Osipova et al. (1976) found significantly reduced spread in single cultivars. Jones et al. (1912) found lesion growth by spread of mycelium in mesophyll well correlated with field resistance. Umaerus (1963, 1970) stated a high correlation between lesion size four days after inoculation in detached leaflets and the number of days to reach 50% by *P. infestans* blighted foliage in the field. Resistance to mycelial spread is examined as the most important component of foliage blight by van Oijen (1992). A genetic correlation was established of r = 0.84 to rAUDPC and IE, r = -0.76 to generation time, r = 0.37 to spore density, and r = 0.83 to spore number per leaflet (Birhman and Singh 1995). However, the leaflets were inoculated by spraying, which could reduce the independence of the components in this excellent analysis. Flier et al. (2003a) found leaf growth rate correlated with foliar disease ratings r = 0.57.

Considerably lower LGR in the field than in laboratory test explains different results for cultivar Golden Wonder (Jeffrey et al. 1962). Cultivar Lama is an example for low LGR (Osipova et al. 1976). Elder cultivars were selected for spread in leaves; new ones are selected mainly for resistance to penetration (Erjefaelt 1975). Chauhan et al. (1999) found in detached leaf test of 60 genotypes of wild species a moderate genotypic coefficient of variation and genetic advance but high heritability.

Sporulation capacity (SC) expresses the component of resistance to sporulation, which is assessed as a snapshot by most authors, for instance three days after inoculation (Singh & Bhattacharyya 1995). It is not sure that stated relations are true for the whole sporangia production of a lesion or a leaflet over time, production on stems is disregarded. Usually the total spore production on leaves or foliage is not considered. However, Weihing and O'Keefe (1962) as well as Bashi et al. (1982) yielded sporangia in intervals of hours and days. Details of related area of the lesion play a rule for correct estimation and real comparability (Umaerus 1970). Assessment of leaflets from field plants by Umaerus and Lihnell (1976) included determination of the leaf area five days after drop inoculation, shaking of 10 leaflets per clone in 20 ml alcohol solution and counting.

Guzman-N. (1964) cut 50 disks from the margin of well developed lesions with a 1-cm cork borer four days after inoculation and placed them for 12 hours in Petri-dishes, before washing in defined amount distilled water and counting. Two inoculum densities in the ratio 1:10 better express this component. Umaerus (1963) counted produced sporangia from disks of 30 mm average. Birhman and Singh (1995) subdivided number of sporangia per lesion and per leaflet after spray-inoculation with 0.025 ml zoospore suspension, calibrated to 15 sporangia per mm^3. SC was determined by cutting out the sporulating area of each leaflet three days after beginning of sporulation. Main and Gallegly (1964) cut 10 disks from 3-4 days incubated detached leaflets and washed the sporangia after 16 hours in a moist chamber. Colon et al. (1995a, b) cut leaflets with well developed lesions after last measuring of LGR on the plant in greenhouse or

field and incubated them 24 hours in the dark in moist chamber. Sporangia number was related to lesion circumference instead of lesion size, calculated as ½ π (length + width of the lesion); counts were ^{e}log transformed. Dorrance et al. (2001) cut a 15-mm disk from the edge of each lesion of three leaflets per clone in the morning, when border rows were 75% blighted to determine SC. Inglish et al. (2007) estimated sporulation per lesion from field-grown pre-breeding material naturally infected from three lesions per plant and three plants per clone on disks 1.4 cm in diameter at the end of vegetation. In case of dry weather conditions leaflets were placed in moist chamber overnight prior to cutting the disks. Carlisle et al. (2002) determined the sporulation density from five leaflets per cultivar and isolate by dividing total spore count by total lesion area in mm^2; the data were transformed to log_{10} for calculation. Spijkerboer et al. (1999) inoculated 10 leaflets per plant, grown eight weeks in greenhouse, incubated the plants one night in moist chamber followed by 70% relative humidity and 15/10°C or 20/15°C. Four and six days after inoculation infected leaflets of three plants per test plot were cut off and incubated in test tubes with water agar in the dark at 100% relative humidity at 20°C for 16 hours. The sporangia were washed off and counted and compared as total number of spores per plant. Bobkova et al. (1982) counted the number of sporangia produced on 25 leaflets per potato clone four days after inoculation in a moist chamber at 19-21°C and calculated per leaflet. However, the size of leaflets differs considerably between clones.

Usually the number of produced sporangia is taken over in a determined volume of water and its density is counted by means of a haemocytometer. Umaerus and Lihnell (1976) counted the conidia in an electronic particle counter of the type Celloscope after some adaptation to the sporangia size.

Haussdoerfer (1959a), Lapwood (1961a), Brock (1967) and Johnson and Taylor (1976) considered this component as result of the whole pathogenesis and therefore as superior component. Schaper (1951), Mueller and Haigh (1953), Deshmukh and Howard (1956), van der Zaag (1956) thought it as very important, Knutson (1962) as the only one component that correlated to resistance in the field. Cultivar Ackersegen produced a fifth of the amount of sporangia of the early cultivar Arran Pilot (Deshmukh and Howard 1956). High SC was correlated with high lesion growth rate (Caten 1970). However, Main and Gallegly (1964) and van Oijen (1992) considered SC as less effective. A genetic correlation of r = 0.84 of resistance in field (rAUDPC) to the number of sporangia per leaflet and of r = 0.58 to the number of sporangia produced per lesion are ascertained by Birhman and Singh (1995). In this case SC and LGR are lesser independent than usually because of the method used. Moreover, sporangia production per leaflet and LGR had the highest direct effect on rAUDPC and high broad sense heritability, but SC had a lower genetic selection advance than LGR (Birhman and Singh 1995). Flier et al. (2003a) found SC correlated with foliar disease ratings r = 0.37. In detached leaf test of 60 genotypes of wild species low genotypic coefficient of variation and genetic advance were stated but high heritability (Chauhan et al. 1999). Dorrance et al. (2001) found a correlation between SC and AUDPC of r = 0.18-0.54. Lower leaves on a plant are more susceptible to lesion expansion, but sporangia production is higher on the upper canopy (Porter et al. 2004).

Instead of SC Gabriel et al. (2007) visually estimated the percentage of the total leaflet area that was sporulating at 168 hours after inoculation of detached leaflets.

Generation time (GT) or better generation interval was assessed already by Vowinckel (1926) as interval between inoculation and beginning of sporangia production as measure of quantitative foliage blight resistance. Deshmukh and Howard (1956) also considered GT an important measure, but named it incubation time; Carlisle et al. (2002) and Gabriel et al. (2007) named it latent period. Colon et al. (1995b) estimated GT as time in days after inoculation at which 50% of the finally achieved number of actually sporulating lesions was reached. From fourth to seventh day after inoculation of intact plants in the field each morning a stripe of cello tape was gently pressed against the lesion on the lower side of the leaf and later observed under a

microscope. Flier and Turkensteen (1999) considered the interval to reach 10% of the total sporulating disks after its direct inoculation. Guzman-N. (1964) cut leaflets from inoculated whole plants, if first symptoms occurred; she placed them in a moist chamber and examined 3-12 hours later in hourly intervals for occurrence of sporangia. Birhman and Singh (1995) recorded GT by scanning leaflets for observation of sporangia 48 hours after inoculation and at following 10-hour intervals. GT was determined as number of hours from inoculation until sporangia first were seen by Singh & Bhattacharyya (1995), but was named the latent period. Cañizares and Forbes (1995) defined GT as the period in days between inoculation and when half the lesions were sporulating. The GT of Bolivian local cultivars based on cultivated potato species ranged from 3½ to six days (Gabriel et al. 2007).

Schaper (1951), Lapwood (1961b), Guzman-N. (1964), and Umaerus (1969a) found that resistant cultivars had a longer GT than susceptible ones. Quantitatively resistant potato clones take longer time to develop a germ tube (Lapwood 1968). From GT an indirect effect via LGR is expected by Birhman and Singh (1995), expressed in high genetic correlation coefficients to all other components (r = -0.76 to -0.97) and rAUDPC (r = -0.79). Low genotypic coefficient of variation and genetic advance but high heritability was stated by Chauhan et al. (1999).

Penetration time (PT) or inoculation period is the duration of leaf wetness after inoculation. Guzman-N. (1964) investigated it by inoculation of plants in greenhouse with zoospore suspension and limiting the duration of drops to 2, 3, 3½ and 4 hours. After 72 hours the number of lesions was counted. For the more susceptible material lesser than four hours were enough for disease development. Main and Gallegly (1964) tested PT of 2-24 hours; 6-10 hours incubation in moist chamber was the best. Lapwood (1968) found seven hours for cultivars assessed sufficiently and explained the longer duration necessary for most resistant ones with different behaviour of the pathogen before penetration (Lapwood 1963). Umaerus (1969a) recorded a minimal PT of five hours for Bintje, nine hours for Ackersegen and 15 hours for better clones. Dorozhkin et al. (1972) considered at least six hours necessary. Umaerus (1969b) applied 15 hours for seedlings selection, Yashina et al. (1974) and Bobkova et al. (1982) used 16 hours.

Incubation time or incubation period (IT) describes the duration of time without symptoms after inoculation. Usually discolouration and necroses are the first signs and occur firstly on more resistant potato clones. Schaper (1951) found a correlation to its field resistance, whilst Guzman-N. (1964) as well as Main and Gallegly (1964) and Lapwood (1968) ascribed this component low importance. For breeding an exact assessment of this component in large scale is to labour-intensively and its information not valuable.

Relations of resistance components with each other are difficult to interpret, they vary in different material as shown by Colon et al. (1995b) and depends from methodical details. Lapwood (1961c) assessed a large scale of cultivars on fife components, but with little practical conclusions. Guzman-N. (1964) found IT the only component without relation to overall resistance. Popkova and Bychenkova (1968) calculated an index for overall resistance from the product of SC time's lesion size after four days plus the same after six days divided by days of IT. The result then was weighted dependently from maturity group of the clone.

Only few investigations went in detail. More research is necessary with complicated bio-statistical analysis. Malcolmson (1969a) found none of the components to prefer for selection of breeding material. Umaerus and Lihnell (1976) measured IE, LGR and SC in laboratory tests and used these parameters to calculate the leave area destroyed by the pathogen after five generations; the resulted ranking order correlated with field observations in both Sweden and Mexico for tested seven cultivars. Nilsson (1981) calculated a correlation between IE and LGR r = 0.63. LGR and SC correlated only in 7/23 cultivar comparisons (Knutson 1962). Entrance into leaf tissue and invasion of it correlated r = 0.63 (Anonymous 1980). IE, LGR and GT were found to be statistically significant indicators of the AUDPC of a collection of *S. phureja* in Ecuador. Cañizares and Forbes (1995) assumed that these three components can be controlled by different genes

which segregate with some independence. Following correlation coefficients were calculated: IE to LGR r = 0.74, IE to GT r = -0.53, and LGR to GT r = -0.38. Gabriel et al. (2007) found LGR best correlated with GT (r = 0.73) and both best correlated with AUDPC (r = 0.53, r = 0.54); relative sporulation area showed r = 0.18 with AUDPC. A low correlation was found between rAUDPC in field assessment and number of days to reach 5% level of foliage blight (r = 0.1-0.6) as well as with SC (r = 0.18-0.54, Dorrance et al. 2001). In old cultivars AUDPC correlated to LGR r = 0.90, to GT r = 0.42 (Colon et al. 1995a). Carlisle et al. (2002) found IE significantly correlated with LGR, GT and SC, GT with LGR and SC in a range of r = 0.23-0.72. They considered calculation of an index as not helpful without more knowledge about relative importance of single components in disease progress.

An example of the relation of the components to rAUDPC is given by Birhman and Singh (1995) in table 14.

Table 14 Phenotypic, genetic and environmental correlation coefficient r of foliage resistance components of 16 potato genotypes to quantitative field resistance (rAUDPC) against *P. infestans* according to Birhman and Singh (1995). IE: infection efficiency, GT: generation time, LGR: lesion size, SD: sporangia produced per lesion, SP: sporangia produced per leaflet.

Component	IE	GT	LGR	SD	SP
Phenotypic r	0.25	-0.57*	0.71*	0.42	0.72**
Genetic r	0.51	-0.79	0.84	0.58	0.84
Environmental r	-0.21	0.27	0.05	-0.24	-0.27

Only for phenotypic correlations significances are declared in table 14. The genetic and environmental correlations correspond to the portioning of the covariance into the additive genetic component *versus* all the rest. LGR and SP had the highest phenotypic and genotypic correlation to resistance in the field, followed by GT. Estimation of heritability and possible selection progress favoured LGR as most effective component. However, Nilsson (1981) found no significant correlation between LGR and blight attack in the field, but r = 0.90-0.92 between IE and blight attack in the field. Pietkiewicz (1976) extensively examined components of resistance of Polish varieties in detached leaf test with spraying or dropping. The widest variation has been found for resistance to spread (LGR); other components variation decreased in following order: % of not infected leaflets, SC, stem resistance and IE. Multiple regression showed that the number of infected plants in field assessment was determined by IE, LGR and SC, whilst the rate of infection in the field depended significantly on LGR and SC. The single components correlated with r = -0.58 to 0.41. On the contrary, number of spots and LGR correlated in material of CIP with r = 0.63, whilst only IE correlated with field resistance r = 0.9 (Anonymous 1980).

Weihing and O'Keefe (1962) selected resistance components on foliage and tubers to predict the resistance of cultivars in epidemiological view of a year. They calculated

1. the primary infection potential (foliage sporangia potential x tuber susceptibility),
2. the foliage sporangial potential (earliness in sporangial yield x maximum of sporangial yield),
3. retention of inoculum potential (rate of mycelial growth in tissues x mycel invasion from leaf to stem.

The authors expect that their method is too complicated for application in breeding; however their thinking should act as a stimulant for comprehensive view in resistance breeding.

4.1.12. Dose-response test for quantitative foliage resistance

Such procedure is described by Kroll and Eide (1981) for field assessment, by Lapwood and McKee (1966) for detached leaf test. The principle is comparison of disease progress of different inoculum densities from a series of inoculum dilutions. Only primary infections are desired; the percentage of blighted foliage is observed up to 10 days after inoculation. The data are presented on log-probability graphs with the log of spore concentration on the X-axis and the percent blight on the Y-axis. The dose-response relationship is characterized by the position and the slope of the regression line. The position depends upon the number of infections and the rate of tissue invasion, while slope (regression coefficient) is due to rate of penetration. New (secondary) infections are avoided by application of fungicides. This method seems to be too pretentiously for breeding concerning the plot size and technique for inoculation.

4.1.13. Passively acting cultivar factors on late blight incidence of foliage

Such factors are epicuticular wax on the leaves, epidermis thickness, stomatal density and stomatal size, number of hairs per unit of leaf area, leaf angle, and plant height. All these factors were examined by Singh and Bhattacharyya (1995), partly in the field and partly on plants grown in greenhouse with four cultivars. Significant clonal differences were found for light intensity passing through the crop canopy, the relative humidity in the crop canopy, the stomatal resistance, the amount of epicuticular wax/100 cm^2 leaf area, number of hairs/ mm^2 and leaf angle. Besides the leaf angle none of these factors correlated significantly with the final result of the cultivars, which underlines that the late blight level results from several more independent factors with mainly small effects.

Pubescence of leaves causes drain off of rain drops on leaves of *S. microdontum* and *S. vernei*, therefore higher disease severity resulted from inoculation by dipping in suspension or infiltration (Zarzycka et al. 1978). Type A trichome density and PPO activity of type A trichome glands correlated negatively to foliage blight severity in assessment of whole plants but not in test of detached leaflets on clones derived from *S. berthaultii* (Lai et al. 2000); a relation to a new R-gene could not be excluded.

The influence of plant architecture (plant high, leaf area index, leaf number) on severity of late blight is objective of a new project (Esnault et al. 2011).

4.1.14. Discriminating R-gene possessing potato clones from such with true quantita tive resistance only by analysing field assessment data

Andrivon et al. (2006) proposed to calculate two additional parameters from data of field assessment to discriminate presumable effects of partly effective R-genes from true quantitative resistance only. The procedure requires at minimum two dates of observation per week to calculate the data sufficiently exactly: 1. delay of epidemic onset in days ($\Delta t = t_{0i} - t_{0s}$) of each clone ($t_{0i}$) compared with cultivar Bintje (t_{0s}) and 2. the reduction of the rate of epidemic progress ($\Delta a = a_i - a_s$, apparent infection rate) of each clone (a_i) compared with cultivar Bintje (a_s), which is calculated from log-transformed AUDPCs. Both parameters for each tested clone are expressed after subtraction of the value for standard Bintje and plotted on the plane defined by Δt as the horizontal axis and Δa as the vertical axis. Two threshold lines are introduced, for Δt considering from observation interval and for Δa as half the value of standard Robijn. The method approximately divides the material in four parts: the highly susceptible part ($\Delta t = \leq 0$, $\Delta a = \geq 0$), the clones on which R-genes affected the result ($\Delta t = > 0$, $\Delta a = \geq 0$), the group in witch probably R-genes together with minor genes acted ($\Delta t = > 0$, $\Delta a = < 0$), and the group with minor genes only ($\Delta t = \leq 0$, $\Delta a < 0$). Examples of application are given by the authors (Andreu et al. 2010). However, correction of maturity effect is much more important for breeding.

4.1.15. Combining of methods in breeding

Umaerus (1970) recommended selection in several steps beginning with seedlings selection for infection efficiency on about eight weeks old plants at 15°C. Selection follows on post infectional components for rapid necrotization and low sporing capacity by single leaf test or test of whole plants in greenhouse. Final checking is conducted as field assessment. Gallegly (1962) assessed and selected in three steps with increasing accuracy: seedlings selection, whole plants test in greenhouse, field test in Mexico.

Early generation selection can be carried out on field transplanted seedlings and single hills during the first two years of potato clones life (Bolvareen & Thill 2005). Quick selection of new cross parents and quick succession of generations was intended. However, the method with one plant per clone is appropriate for selection to hypersensitivity only. Success of application of quantitative resistance depends on high priority of late blight resistance with appropriate methods and consideration of all important other traits in each generation, mainly of the polygenic determined ones. Not speed in breeding decided success or run aground but balanced accumulation of polygenes for several traits at the same time.

Our selection system includes seedlings, test of detached leaves from A-, B-, C-, D-clones and field assessment of B-, C-, and D-clones. Last step could be conducted one year earlier (3.-5. year in clone life).

4.1.16. Components of foliage resistance behaviour with special interest for recommendations of oomycide application

The interest on the characterization of foliage blight resistance is in detail not identically for breeding and for chemical plant protection. Whilst breeding requires a description independent from maturity, operational recommendations for oomycide application need reliable information on cultivar-specific disease progress suitable for saving of chemical ingredients and low-risky disease forecast. Kessel et al. (2003) wrote: "Apparently, resistance ratings from the Dutch national variety list are ill suited as a base for recommending reduced dose rates on more resistant cultivars. A more solid base for dose rate recommendations is urgently needed." Spits et al. (2004) selected infection efficiency (IE) as most important component of cultivar resistance from five components (Kessel et al. 2004) to compliment by chemical protection. Hansen et al. (2002a) used delay of first symptoms and relative apparent infection rate (AIR) as important information concerning cultivar resistance in comparison to a standard cultivar. Perhaps it is most meaningful to make reference to an early standard variety, otherwise a high susceptible standard cultivar in each maturity group would be necessary. Chatot and Bersihand (2004) applied the same components. Cultivar-specific adaptation of reduced chemical input according to the level of resistance is best possible considering expected delay and AIR, because similar AUDPC can result from very different combination of delay and AIR (Chatot and Bersihand 2004). Both trait components are used in 4.1.13. too; its calculation from the raw data is easy and available in www.eucablight.org, however at least two weekly field observations are necessary.

Potato cultivar breeding should be highly interested to hold ready these information's for plant protection to use cultivars late blight resistance as competitive advantage and contribution for pollution control. Therefore cooperation with specialists of plant protection is necessary. Already Fry (1975) demonstrated the value of late blight resistance of cultivars in term of oomycide equivalent. Nærstad (2001) developed a formula to describe the relationship between the effect of resistance and oomicyde on the disease level. Reduction in oomicyde dosage was better than of frequency of applications.

It seems that structural changing of potato growing supports more and more a simple spray schedule with cultivar-specific variation of dosage (Cooke et al. 2011a). Then risk of protection and chance of saving chemicals depend from reliability of assessment of resistance on foliage and tubers; both are considered in Decision Support Systems (DSS) for operative integrated late blight control management.

4.2. Methods of assessment of foliage blight resistance at ZL Gross Luesewitz

At Gross Luesewitz seedlings selection is followed by single leave test and field assessment. Pre-breeding for quantitative late blight resistance at Gross Luesewitz was planned to support by suitable methods at the end of 1950ies. Detached leaf test was introduced by Haussdoerfer (1959a). During following years mainly three methods of assessment of foliage blight resistance were applied at the Institute Gross Luesewitz: Seedlings selection as the first step, single leaf test for characterization of the resistance type and components followed by careful selection, and finally field assessment. Generally a mix of three isolates with highest available combination of virulence genes 1 to 11 was used, in past for instance 1.2.3.4.5.6.7.9.10.11 or 1.2.3.4.5.6.7.8.9.10.11 from culture on tuber slices for all inoculations to minimise the cultivar/isolate interaction. Our decision did not agree with the majority of colleagues, but the results of Flier (2001) and Carlisle et al. (2002) support our procedure. Additionally, taking new isolates from most resistant clones (including R8 and R9) in the breeding garden at the end of vegetation as candidates for inoculum (after assessment on differentials) meets requirement for highest virulence combination as well as high aggressiveness. Each of the isolates in the mix has to be compatible, of course.

Usually different persons are responsible for assessment of resistance and breeding in other countries. Responsibility of the author for both made pressure from insufficient results in breeding to develop high activities for minimizing shortcomings concerning methods of assessment of resistance and of breeding. Integrative solutions were the key of our progress in pre-breeding for long day conditions.

4.2.1. Seedlings selection for foliage blight resistance at ZL Gross Luesewitz

All seedlings (fig. 15) are planted on a distance of about three cm 8-12 days after emergence (fig. 16) to reach uniform growth and enable discarding of single plants without damaging the neighbours in selection against too high susceptibility. Additional 10-14 days later they are inoculated by spraying with spores of *P. infestans* in stage of 4-6 leaves (Oertel 1972, Darsow & Oertel 1986, Darsow 1988b, Darsow 2000a). Suspension with 10,000-15,000 sporangia/ml is used at the evening after staying two to three ours at 8°C for zoospore release. Spraying was conducted with low pressure-device. Seedlings were substantial watered few hours before inoculation. Immediately after inoculation plants were covered with polyethylene awning for about 14 hours to ensure 100% air moisture at 16-22°C. Later usual air conditions occurred in greenhouse. Selection started nearly 84 hours after inoculation. Plants with >15% necrotic leaf area or with necroses on the under stem part are discarded (Darsow 1992b). Plant height increases powerfully from inoculation to selection date (fig. 17). During sporulation of *P. infestans* on seedlings contact with water is avoided.

Preparing best seedlings for potting on the following day includes removing of infested leaves of plants with score 8 or 7 and sometimes cutting of stems below necrosis. Each seedling is to control for symptoms again immediately before potting and on the following four days. Plants cut above the first (lowest) node regenerate, if the pathogen was not advanced into the stem basis. A fungicide application on day of potting and four days later reduces dying of plants and should eradicate the pathogen in greenhouse. A susceptible selfing population served as control representing cultivar level on each date of inoculation. Additionally this population is used as susceptible standard in seedlings test for tuber blight resistance, grown from non-inoculated additional plants. The number of seedlings per date of foliage inoculation depends on stuff to finish selection on one day and on area in greenhouse to guarantee 100% air moisture after inoculation.

Our investigation of the representativety of seedlings reaction for their foliage blight resistance

in the field (considering all components of resistance) based on 838 identical individuals of 11 populations in groups from highly susceptible to very highly resistant tested three consecutive years (compare table 3). Among remaining seedlings with score >6.4 on the 1-9 scale of falling infestation about 89% of individuals with good resistance in the field were correctly kept by seedlings selection and 64% of the seedlings too susceptible in field were correctly discarded (Darsow 1992b). At the same time 14% of individuals with sufficient tuber resistance in the slice test were lost by seedlings selection for foliage blight resistance (Darsow 1992a). The risk increases with advance of pre-breeding from the source of resistance, our results stands for BC5 (backcross five). Too high temperature in greenhouse can cause low infection. The elder the plants the lower is the risk of too heavy infestation.

4.2.2. Detached leaflets test of foliage blight resistance at ZL Gross Luesewitz

In pre-breeding single leave-test is used from material grown in the field without oomycides at the end of June or beginning of July and from plants (single healthy ones) grown in greenhouse for testing of virus infections in February. A-clones (second year in the field) and elder clones are tested up to four years. Components of foliage blight resistance as infection efficiency, lesion size and sporulation intensity could be established separately with impressive differences from about 500 clones per year. Occurrence of sporulation on the best clones is more intended to exclude hypersensitivity than an overall-test.

To test several hundreds of clones, at Gross Luesewitz earlier seven, now five leaflets are taken of the first to second full developed leaf, each leaflet from another plant between 8.00 und 11.00 o'clock. The leaflets are put in boxes according to Schick und Hopfe (1962, see fig. 32). Wooden frames have a bottom from gauze on moist filter paper and are closed by a pane of glass. These boxes enable limited air exchange. About 15 sporangia/mm^3 coincide with 90,000-100,000 zoospores/ml. The leaflets are usually inoculated with one drop of 20µ on the underside of each leaflet. The leaflets are incubated on 16-19°C and 95-75% air humidity most days, 95-100% during first and last 14 hours. 16 hours day light are given. One day after inoculation the leaflets are turned over, 116-124 hours past inoculation as well lesion area as area and density of sporophores with sporangia are visually estimated by means of a stereo microscope. Generally upper and underside of the leaves are observed for sporulation, leaflets given scores 1-4 are observed on the underside only. Very intensive development of aerial mycelium is shown in figure 18. Already few spore-bearing sporangiophores make score 8 and show probably compatible host/pathogen relationship. Sporangiophores rotate as on a ball bearing in gentle air stream. Because density and area of sporangiophores are to consider, table 15 gives only approximate values for estimation of sporangiophores. Necroses with score 8 (see fig. 13) or 7 (see fig. 14) are sharply delimitated from healthy tissue. An example for score 6 is given in figure 19. Because of different size of the leaflets of breeding material a template with a cut of 6 cm^2 helps to score correctly.

Table 15 Scale for estimation of infestation in assessment detached leaflets related to 6 cm^2

Score	9	8	7	6	5	4	3	2	1
Sporangiophores	0	0.5%	4%	10%	30%	55%	75%	87%	97%
Blemish	0	3 mm	9 mm	12%	25%	50%	67%	83%	95%

The score of resistance is calculated from main value of score for sporangiophores and for blemish. A correction by regression to maturity is not tried up till now. Drop inoculation considers mainly growth of mycelium in leaf tissue and intensity of sporulation. Infection efficiency is better tested by spraying and using two densities of inoculum in parallel.

Year of testing, age of plants, high of insertion of the leaf, water supply, day length, hours of sunshine the days before testing and other diseases influence the resistance isolate-specifically and clone-specifically (Darsow et al. 1988). The own research urged to selection with care. Selection in pre-breeding considered statistically assessment data of different years. Standard cultivars (see 4.2.3.) and simple differentials according to Black from SASA Edinburgh (r, R1, R2 … R11) are included in each test. The results of detached leaflets of 245 pre-breeding clones correlated to field assessment with r = 0.75 in 1995. Therefore in pre-breeding only careful negative selection is conducted according to the results. Important is to characterize additionally the foliage resistance of the best part of clones (from field test) in its components of % leaflets without lesion growth, the average of lesion growth and sporulation intensity, and this at the end of flowering or a bit later, which is the most relevant (critical) period in practice (Mueller 1931).

The material of the gene bank Gross Luesewitz of IPK Gatersleben (GLKS) has been assessed by ZL with test of detached leaflets and drop inoculation from its beginning (Darsow et al. 2002).

4.2.3. Field assessment of foliage blight resistance at ZL Gross Luesewitz

Gross Luesewitz is a location with frequently dew, mist and rain and therefore suitable for field assessment of foliage blight resistance. Even in a year with long summer dryness as 2006 it was possible here to inoculate successfully and make sure progress of disease for normal selection. Figure 20 demonstrates that on relative heritability of percent foliage incidence values calculated for single scoring dates in average of 854 genotypes in the years 2004, 2005, and 2006. Sufficient durability of droplets of water on leaves is supported by a simple sprinkler irrigation system and by sheltering from wind by hemp (fig. 21, fig. 22).

An important measure to reduce falsifying effects from neighbours is grouping of clones of similar maturity together and in maturity groups, if known, clones of similar resistance level as sub-groups together. Distribution by chance is applied within the sub-groups only. Up to now the material is split in two maturity groups: 1. early to second early, 2. last part of second early to late. Two fields in a distance of ≥50m would be better than growing on the same field, the later group placed against the main direction of the wind. Separated fields enable two different dates of inoculation with better adaptation to the right physiological stage of the host. According to our experience in the described design size and shape of the plot are more important than replications. Plots of three rows with six plants each are sufficiently, two replications are enough. One replication with three rows per plot is better than three replications of single rows. The data are collected mainly in the middle row. Plots of one or two plants deviate from the normal reaction. Even with plots of four plants in our practice two replications were found to be enough (fig. 8) and more than three years had no advantage (fig. 9).

The field is inoculated one times in the period of July, 5-12. Rainy weather should be elected for that, otherwise inoculation past 20.00 o'clock is most successfully. The problem is that subculture of the pathogen for inoculum has a rhythm of six to seven days with a margin of maximal one day to deviate according to the weather. Higher deviation requires decision two weeks in advance, longer than the weather forecast is to get reliable enough. We inoculate each clone on two leaves of one plant per plot (Darsow 2000a, Darsow 2003a), formerly on two stems (Darsow 1989a). Minimized local inoculation increases polycyclic the part of auto-infections, delays neighbour infections and expresses better the genotypic differences of foliage blight resistance in all its components than inoculation of the whole plot or natural infection.

Two leaves near the surface of the ground of the first or second plant of the middle row on

the northern side of the plot are sprayed on the underside. Such leaves are mostly protected against wind and sunshine. More than seven hours duration of the droplets with zoospores is guaranteed and most favoured conditions are given for infection and disease development. Careful inoculation of the underside means a physical exertion, even with a suitable spray pipe, and is much more important than the inoculum density; 5,000–30,000 sporangia/ml are preferred, counted before its release of zoospores. Disease progress is supported by irrigation. Irrigation near clock 7 in the morning and about 1-2 hours before development of mist or dew in the evening is helpful in dry periods; applications near midday reduce mainly heat stress of the plants.

Two to three times a week symptoms of blight are estimated as % of blighted foliage or with scores according to table 16. At minimum three observations between 0.5 and 99% blight allow the calculation of apparent infection rate and delay of epidemic onset compared with Bintje according to Andrivon et al. (2006). Score 8.6 means at minimum one sporulating leaflet per 18 plants and a compatible host-pathogen interaction in the 9-1 scale of increasing disease level. Deviating from usual instructions our scale included stem infections too, 100% blighted leaf area corresponds to score 1.8. Symptoms on stems in early stage get a weight three to five time's higher than the same area on leaves.

Table 16 Part of the conversion table for foliage blight infestation in the field with 18 plants per clone using scores or percent of invaded leaves and stems.

Score	8.6	8.0	7.5	7.0	6.5	6.0	5.5	5.0	---	2.0	1.0
% of infested haulm	0.01	1.7	4.4	9.4	16.9	26.2	35.7	45.2	---	96.4	100

Standard cultivars are used for long time to compare result of different years. Such standards of the early to second early group with expected scores of resistance (in brackets) are Eersteling (1-2), Karlena (3), Adretta (2-3), Gloria (3-4), Resy (6). In the second group Bintje (2-3), Cara (4-5), Panda (5-6), Kuras (6-7), Sarpo Mira (8-9) were used. Some highly resistant pre-breeding clones additionally are employed. These standards are grown with three replications of 18 plants, the differentials (r, R1, R2 … R11) only once with up to six plants. The maturity of the potato clones has to be evaluated in another trail (nearly) without diseases in average of two or more years for calculation of regression rAUDPC/maturity (see 4.2.4).

Components of resistance as resistance to spread and sporulation intensity (fig. 23) sometimes may be observed in the field in very suitable weather conditions early in the morning. These components of resistance are considered in addition to results of single-leaf test for combining of complementary components by inter-crossing. Resistance to infection dominates in our material. It protects up to a certain stage of maturation (Darsow 2000a).

Detailed recommendations were given for field assessment of foliage blight resistance of statutory evaluation of cultivar candidates before inclusion on the national list by Bundessortenamt of Germany (Darsow 2003a).

Assessment of wild material in the field has the problem of late emergence and slow haulm development, which causes not a suitable microclimate for late blight in July and August. Nevertheless, some clones of PD-population (*S. phureja* x *S. tuberosum* ssp. *tuberosum*) from B. Trognitz, CIP, showed early sporulating incidence on stems and petioles long time before leaf infections (fig. 24).

4.2.4. Quantitative foliage blight resistance and maturity at ZL Gross Luesewitz

Infection frequency and disease progress are influenced by physiological state of host (maturity) and real resistance. The mix of both, foliage resistance and maturity effect is not to handle as trait in breeding, but is usually used as synonym for resistance. Already Schaper (1949) and Schick et al. (1958b) considered the connection of quantitative resistance and lateness as problem solvable by breeding.

Foliage blight severity in a population is not often so even distributed as in figure 25 with 130 clones and no doubt concerning compatible host-pathogen interaction. Next example is more commonly (fig. 26). Calculation of resistance requires data of disease progress and maturity as exactly as possible. The following table 17 shows results of calculation of some parameters with different methods. Foliage blight resistance GL (FBR_{GL}) results from an empirical method applied by Darsow (1989b) since 1984 and is repeated described in Darsow and Hansen (2004), which calculated the resistance for a test set of several hundreds of clones from a section of the disease progress curve of each clone according to its maturity. The section was empirically decided firstly for several standard clones and fixed for its maturity score. In next step the calendar period for maturity data between 9.0 (extremely early) and 1.0 (extremely late; latest tested cultivar got 2.4) was fixed by interpolation. The daily average of disease level in this section (period) results the resistance score. This section included 3-5 days for very early material and expanded to about 20 days in late clones. The correlation coefficient should be below 0.15 and the standard cultivars in each maturity group should get nearly the expected value of resistance. Otherwise for repeated calculation the section is started a day earlier, or its steps of prolonging and shifting to later dates with later maturity are changed. The procedure was repeated so long till the preconditions were fulfilled.

Table 17 Correlation between parameters of resistance and maturity in assessment of 2003, calculated with 27 varieties and one pre-breeding clone (Darsow & Hansen 2004). FBR_{GL} results from empirical calculation of foliage blight resistance.

Trait 1	Trait 2	Coefficient of correlation r	r^2x100
Maturity	FBR_{GL}	-0.1804481	3.3
Maturity	AIR	0.7219806	52.1
Maturity	rAUDPC	0.53410955	28.5
Maturity	Delay of attack	-0.68751873	47.3
Maturity	Attack 08.08.03	0.69948184	48.9
FBR_{GL}	AIR	-0.68084469	46.4
FBR_{GL}	rAUDPC	-0.64983314	42.2
FBR_{GL}	Delay of attack	0.61259319	37.5
FBR_{GL}	Attack 08.08.03	-0.72303192	52.3
AIR	rAUDPC	0.59432455	35.3
AIR	Delay of attack	-0.86462902	74.8
AIR	Attack 08.08.03	0.97986814	96.0
rAUDPC	Delay of attack	-0.58310141	34.0
rAUDPC	Attack 08.08.03	0.62862649	39.5
Delay of attack	Attack 08.08.03	-0.87061444	75.8

AIR (apparent infection rate) and rAUDPC (relative area under the disease progress curve) are scientific standard to calculate foliage blight resistance (www.eucablight.org, Darsow & Hansen 2004). All correlation coefficients in table 17 proved to be significantly, except between maturity and FBR_{GL}, in which foliage blight resistance was determined by maturity with only 3%. AIR, delay of attack and attack on August 8 as a date with highest differentiation of the tested cultivars can be explained to 47-52 % by maturity. The rAUDPC correlated lower with maturity, r = 0.53. On the other hand rAUDPC, AIR and delay of attack could explain the resistance FBR_{GL} to lower than 50% and do not represent true resistance sufficiently for breeding purpose. Therefore rAUDPC means a little progress compared with AIR and AUDPC, but is not suitable to improve successfully quantitative late blight resistance in potato breeding; but that is common qualified practice (see 2.5.).

Gross Luesewitz was for about 20 years the only one location, at which separation of both traits was carried out in past. Two populations best show the effect of calculation of resistance in contrast to disease level in relation to maturity. Both were assessed in the special field with four plants in two replications each three consecutive years with 250 and 310 clones, respectively. Severity of foliage blight was strongly correlated with lateness (score 1: extremely late; fig. 27, fig. 28). Quite different distribution resulted from elimination of maturity influence by calculation of the resistance (fig. 29, fig. 30). Over four populations (854 clones) foliage blight resistance and maturity correlated r = 0.046 in 2004 (FBR_{GL}).

To separate the resistance from the maturity effect, since 2005 a linear least-square regression was calculated for tested pre-breeding material each year (Darsow & Strahwald, 2006, unpublished, Truberg et al. 2009). This calculation is applied by Bormann et al. (2004) and by Bradshaw et al. (2004a) in molecular-genetic research, but up to 2006 not for practical purpose outside of Pflanzenzucht SaKa GBR Windeby. In figure 31 rAUDPC of 27 cultivars is shown, tested at ILK Gross Luesewitz in framework of EUCABLIGHT and arranged according to its maturity. The rAUDPC-values were multiplied by 100 and entered in distance to X-axis. Instead of the rAUDPC-values its vertical distance to the regression line with maturity, for instances a (susceptible) and b (resistant), is the recommended criterion of foliage blight resistance. A rAUDPC-value of 0.5 of a second late (maturity 3) cultivar in figure 31 corresponds with rAUDPC = 0.85 of an early cultivar (maturity 7); both have the same level of resistance, because they are situated on the regression line; its difference is caused only by maturity, but is usually explained as different "resistant" in common practice and literature. The vertical distances of rAUDPC to the regression line are uncorrelated to maturity and appear as useful measure of true foliage blight resistance. Its conversion to scores in a 1-9-scale can also be applied in breeding. A similar calculation was applied for early blight resistance by Caligari and Nachmias (1988).

Additional best linear unbiased prediction (BLUP) technique was compared with vertical distance of rAUDPC to the regression line with maturity (Truberg et al. 2009). The BLUP technique has lesser theoretical assumptions for calculation in SAS PROC MIXED; a determined maturity stage gives the final assessment date for AUDPC as proposed by Emrich et al. (2008) for winter wheat/*Fusarium* incidence, variance stabilizing transformation of AUDPC values to x^3 was carried out before calculation. Exact identification of maturity is crucially as in formerly used own method.

'Maturity-corrected resistance' is a new non-sense term which emphasized the right calculation from disease severity, but means true resistance in opposite to "resistance".

A maturity-correction in assessment of detached leaflets should be examined.

4.3. Methods of assessment of tuber blight resistance

Using of trails grown for assessment of foliage blight resistance also for tuber blight "resistance" as described by Howard et al. (1976), Flier et al. (2003a), Rogozina and Patrikeyeva (2004), Porter et al. (2004), Rahkonen et al. (2006) or Whitworth et al. (2007) is excluded as pointless as discussed in chapter 2.8. Tuber blight resistance has a low part in realized tuber infections under such conditions.

All assessing of tuber blight resistance aimed at prediction of defence behaviour representative of an intended growing region. A low to middle genetic variance in assessment on differrent locations and different years results in partly different ranking of clones (Darsow 1987a). Therefore methods striving to consider largely field conditions are most valuable for finally selection of breeding material. The methods applied to assess quantitative tuber blight differ in

1. focussing on resistance to entrance or
2. resistance to spread by regarding wounds as infection site,
3. striving to consider largely field conditions,
4. duration of storage before inoculation,
5. considering wound healing between cutting and inoculation.

Reviews of the methods are given by Schoeber (1987), Wastie (1991), Dorrance and Inglish (1998), and Schoeber-Butin (2001).

The intention to assess tuber blight resistance as early as possible comes into conflict with low available tuber number and requirement of seed potatoes. For characterization of a cultivar in field growing perhaps one method is sufficient (Darsow 2003a), whilst for breeding a system of different methods is beneficially to assess components of resistance (Darsow 2000a). Jellis (1974) recommended the following system of different methods in breeding: 1. detecting and rejecting clones with highest growth rate in the medulla by tuber slice test on young material, 2. whole tuber testing with inoculation of eyes on material 4-5 years old, 3. test of variety-candidates in field assessment.

Usually practice and details concerning pathogen culture, preparing inoculum, virulence and aggressiveness of used isolates and evaluation of disease level, and use of differentials and standard cultivars are similar as discussed in chapter 4.1., are partly considered in 2.1., 2.7., and 2.8., and will not be repeated here. Only Flier (2001), Flier and co-authors (1999, 2001a, 2003a) used sporangia suspension at 18°C 30 minutes after preparing without chilling for hatch of zoospores. In pre-breeding for hypersensitivity already tubers from cuttings of seedlings during the first winter were assessed for tuber resistance by Lehmann (1938b) or from second year seedlings by Mueller since 1938 (Mueller et al. 1955).

Slice test of tubers for quantitative late blight resistance should be done from trails in which the vegetation naturally is finished. Adaptation of the inoculum density has mainly to consider the course of soil moisture before harvest in case of whole tubers, and for slice test the physiological stage of tubers (dormancy stage) at the moment of inoculation.

4.3.1. Field assessment of tuber blight resistance

The principle of the method is common growing of potatoes without any incidence of foliage blight, premature haulm pulling and inoculation of the tubers in the ridge. Such tuber test is described by Colon and Budding (1988) and is applied only in Denmark (Colon et al. 2004c in www.eucablight.org). The late maturing group is planted first, the second-early group 21 days later, early material 42 days later, all with two replications of fife plants at minimum. The foliage is cut off on day of inoculation. 50 000 zoospores per ml of a complex race are poured on

the ridge, one litre on five plants in the evening, additional sprinkling or spraying wets the soil. Three weeks later tubers are harvested, washed, observed for symptoms and counted. Symptom-less tubers are stored at 16-18°C following 2-3 weeks for repeated scoring; percentage of attacked tubers are used as measure of resistance. Problems are to get comparable maturity stage of all material at the moment of inoculation (three groups for a continuous variation), necessity to refill high amounts of water in dry years, avoid any foliage infections without to influence infections of tubers in the following test (applying only protectants), recognize the primary pathogen on rotten tubers, and inevitable influence of length of stolones and tuber position in the ridge. Colon and Budding (1988) opened the soil with a fork before inoculation. Their result correlated to the tuber blight resistance in the Netherlands variety list with r = -0.77 and to a laboratory method in parallel with harvest and immediately placing in moist peat and inoculation by spraying with r = -0.88.

4.3.2. Cultivation and assessment of tuber blight resistance under controlled conditions

Plants are cultivated in greenhouse in pots; after harvest inoculation follows with incubation in a moist chamber (Lacey 1967a, Lapwood 1967, Stewart & Wastie 1978/79, see 4.3.3.2). However, a special pot for potato cultivation with a hollow to observe tuberization and tuber growing, easy to open and completely closed, is described by Engel and Raeuber (1960). Tubers are laying free for inoculation or measurements. Using such pots anyone standardization not only of conditions after inoculation but also of growing are possible. Such pots were used by Darsow and Meinl (1981a, b). They are very suitable for research concerning tuber blight resistance, but for large scale assessment there are two problems: 1. high expenditure of work is required and 2. which standardization of growing conditions before inoculation should be chosen?

4.3.3. Assessment of undamaged, whole tubers blight resistance

4.3.3.1 Field-grown tubers

Resistance to entrance is mainly tested on whole tubers and intends to exclude visible wounds. However, skinning or injury of only a few millimetres deep, which occur by gentle harvest or transport technique, is considered in whole tuber test too. Tubers are carefully lifted (frequently by hand to reduce damage) before they are fully mature (early to mid-August in Central Europe, see 2.8.) because of several reasons too: 1. necessity to avoid natural tuber infections, 2. compete with potato harvest at all. Usually tubers are washed before inoculation (Weihing & O'Keefe 1962, Walmsley-Woodward & Lewis 1977, Lacey 1967a, Osipova & Ligay 1978, Darsow 1983a, Stewart et al. 1983b, Chatot et al. 1995, Platt & Tai 1998) but washing resulted in more diseased tuber tissue than unwashed (Clulow et al. 1995, Lozoya-Saldaña & Caballero 2000). Already Mooi (1964), Monson and Eide (1964), Howard (1965), and Lapwood (1967) pointed out that because of high variation within a tuber sample many tubers per potato clone (40-50) have to be tested. The authors used per clone a number of five tubers (Antonov 1970) six (Inglish et al. 2007), 10 (Førsund & Roer 1964), 12-24 (Mooi 1964), 4x15 (Erokhina et al. 1979, Platt & Tai 1998), 20 (Lacey 1967a), 4 x 20 tubers (Carnegie & Cameron 2001), 25 (Stewart et al. 1983b), 20-40 (Stewart & Solomon-Blackburn 2004), 30 (Darsow 1983a, Andreu et al. 2010), or 50 tubers (Dowley et al. 1991). Often few (2-3) days for wound healing were given between digging and inoculation (Lacey 1967a, Walmsley-Woodward & Lewis 1977, Osipova & Ligay 1978), or longer (Howard 1965, Erokhina et al. 1979, Dowley et al. 1991, Chatot et al. 1995, Platt & Tai 1998, Andreu et al. 2010). Partly was tried to restore the tuber state in soil by placing in moist peat or moist chamber several days before inoculation (Mooi 1964, Førsund & Roer 1964, Antonov 1970) or pre-immerse the tubers in water two hours before inoculation (Sato 1995). However,

following Mooi (1964), Stewart et al. (1983b) showed that inoculation at the day of harvest best represented tuber state in soil, only few days later different results are obtained. The tubers were placed rose end uppermost in plastic boxes to inoculate eyes and lenticels mainly and ignore heel-end infections with longest inoculum contact (Stewart & Solomon-Blackburn 2004).

Lacey (1967a) found that the mode of inoculation influenced the result by being conductive to infection via eyes (local inoculation with disks of filter paper or into a Vaseline ring) or lenticels (spraying the whole tuber). Tubers were sprayed in most cases; dipping in spore suspension was used by Bonde et al. (1940), Erokhina et al. (1979), Darsow (1983a), Platt and Tai (1998) and Osipova and Ligay (1978). Ullrich (1964), Pietkiewicz (1976), Lozoya-Saldaña and Caballero (2000) and Rodríguez et al. (2009) inoculated eyes. Duration of inoculum contact of seven hours on eyes at 15°C made 20% infections (Lapwood 1977). Inoculum densities of 10^5 sporangia per ml (Walmsley-Woodward & Lewis 1977), 1.5 x 10^4 (Lapwood 1967), 2 x 10^4 (Flier et al. 1998, Rodríguez et al. 2009), 10^4 (Platt & Tai 1998, Lozoya-Saldaña & Caballero 2000, Inglish et al. 2007), 5 x 10^3 (Dowley et al. 1991), and 2 x 10^3 (Darsow 2004/05a, Andreu et al. 2010) were used of a highly virulent isolate or a mix of different highly virulent isolates. 5 x 10^4 zoospores per ml suspension applied Stewart et al (1983b) and Chatot et al. (1995). First 15-24 hours 95-100% relative humidity and 15-18°C prevailed in controlled moist chambers or in moist peat or sawdust. Then usually followed incubation in normal air moisture and temperature of 18°C for 10 days in the dark (Dowley et al. 1991), two weeks at 12-18°C (Stewart et al. 1983b) or 15°C (Chatot et al. 1995, Rodríguez et al. 2009), 10-14 days at 15-22°C (Stewart & Solomon-Blackburn 2004), 15 days at 18-20°C (Erokhina et al. (1979), 30 days at 12°C (Platt & Tai 1998), 30 days at 15-18°C (Osipova & Ligay 1978), 20 days at 15°C (Andreu et al. 2010), 55 days at 9°C (Inglish et al. 2007), or up to 30 days with three dates of observation (Darsow 2004/05a).

The severity of tuber blight is estimated in different manner. Lapwood (1967) recommended the weighted part of invaded tuber tissue as the best measure of tuber resistance instead of the number of infection points. Rahkonen et al. (2006) did so. Mainly only percentage of infected tubers is used as criterion of resistance (Mooi 1964, Stewart et al. 1983b, Gans & Wooster 1987, Chatot et al. 1995, Stewart & Solomon-Blackburn 2004). Infections due to wounds and through stolon scars are ignored in SCRI. Resistance to entrance and resistance to spread of mycelium within the tubers, both were considered by Darsow (1983a, 2004/05a) for calculation of an index from the number of tubers in nine classes of disease level weighted according to the date of observation. Erokhina et al. (1979) cut the tubers after 16 days and placed them in a moist chamber to estimate % of necrotic cut surface, surface cover with aerial mycelium (%) and percentage of blighted tubers. Osipova and Ligay (1978) calculated an index from superficial symptoms and depth of mycelium penetration into the tuber. Inglish et al. (2007) considered discolouration of cut tuber quarters only. Flier et al. (1998, 2001a) counted infected tubers and scored disease severity on cut tubers on a scale 1-5. For breeding purpose values in percent or index are transformed to a 1-9 scale of increasing resistance (Gans & Wooster 1987). Stewart and Wastie (1989) consider a glance score for a sample of 10-25 tubers compared with standard cultivars as sufficient for breeding purpose; the result correlated to 1. estimation of superficial covering of symptoms and depth of penetration, 2. percentage of infected tubers, with r = 0.7-0.9. For discussion see chapter 2.8. Often the data did not agree with field incidence followed foliage blight (Flier 2001), which is understandable and intended.

4.3.3.2. Tubers grown in greenhouse

Environmental conditions and ontogenic stage influence the preferred site of entrance and disease level of tubers (see chapter 2.8). One possibility to reduce the high variability of defence reaction within a potato sample of a cultivar is standardization of the growing conditions by cultivation in greenhouse, assessing of tuber blight resistance follows as described in 4.3.3.1. Lapwood (1967) cultivated the plants in pots of 30 cm diameter, spray-inoculated tubers were placed on moist peat in closed plastic boxes at 15°C, its observation followed six and 14 days later. The part of invaded tuber tissue was weighed.

Unwounded tubers from smaller pots were used by Wastie et al. (1987, 1993) and applied for advanced breeder's selections (Stewart et al. 1996). For a clonal test replicated samples of 20 glasshouse-grown tubers from flowering plants grown from tubers in 10 cm pots are harvested, washed and dipped in a suspension of 2.5 x 10^4 zoospores per ml on day of harvest, incubated 10-14 days at 15-22°C, first 24 hours at very high humidity. The percentage of the number of blighted tubers is recorded, infections through wounds or stolon scars are ignored (Stewart & Solomon-Blackburn 2004). Dry soil conditions in the pots during three weeks before harvest increase the susceptibility of tubers for late blight infections. Therefore normal water supply should be given up to the harvest (Stewart et al. 1993). The assessment of a clone for tuber blight on glasshouse-produced tubers is lesser accurate than the field test on foliage of SCRI (Stewart et al. 1994).

Tuber blight progeny test in SCRI is carried out on one tuber per seedling raised in 10 cm pots in greenhouse, harvested at flowering. Two samples of 25 tubers per family are tested as described for the clonal test (of potential cross parents and cultivar candidates) on glasshouse-grown tubers (Stewart & Solomon-Blackburn 2004).

Non-wounding assay was applied on tubers of wild species grown in greenhouse by spraying of suspension with 7.5 x 10^4 sporangia/ml; the percentage of blighted tubers after 34 days at 12°C was recorded (Liu & Halterman 2009).

Using of glasshouse-grown seedlings tubers has been introduced for assessment of tuber blight resistance as a rough first selection step in pre-breeding and for evaluation of gene bank material by Oertel (1972). From 1-4 tubers per seedling with 1-3 cm in average a top of 2-4 mm were cut, the tuber dipped in suspension and incubated at 20-23°C in a dark moist chamber for 160-170 hours. Aerial mycelium on the cut surface as well as superficial browning and browning of tissue after cutting of the small tubers was scored 1-9; the most 'susceptible' value of both was used for characterization and selection. Assessment of 6,000 seedlings took a month. Similarly continued Darsow (1988b, 1992a, see 4.4.1.). Dorozhkin and Kazak (1981) used inoculation of seedlings tubers directly for selection of breeding material (without separate seed tuber); only tubers apparently free of tuber blight were planted in the following year and resulted in higher frequency of resistant clones on foliage and tubers compared with not pre-selected population parts.

Zoteyeva (2005) inoculated very little tubers of wild species after cutting the rose end by a drop of suspension on cut surface. Intensity of aerial mycelium on cut surface and depth of penetration visible on longitudinal cut were scored, both 10 days after inoculation. However, additionally field observation without inoculation was used for estimation of foliage and tuber incidence of gene bank material.

4.3.4. Assessment of damaged tubers or parts of the tuber

Potato tissue (halves, slices, or inoculation in a hollow) has been used for cultivation of *P. infestans* or production of inoculum for long time. Testing of R-gene reaction by inoculation on tuber medulla was most suitable. Thereby quantitative differences in disease level between cultivars were stated. Resistance to penetration plays a subordinated or not any role in these methods. Mycelium growth is measurable or visually rated as area of necrotic tissue or aerial mycelium; intensity of sporulation can be established. That way assessment of damaged tuber tissue has longest tradition. The advantages of assessment of damaged tuber tissue are: better reproducibility of the results, lesser tuber number has been required and possibility to assess during storage period. That makes these methods attractive. One argument for inoculation of wounded tissue is that at an eye the vascular elements and medulla approach the tuber surface, infections through the eye may allow direct access to the central susceptible tissue (Lapwood 1965). The frequency of tuber injury during harvest, transport and storage and its depth are another argument for or against these methods.

4.3.4.1. Assessment of damaged, whole tubers late blight resistance

Compared with methods mentioned under 4.3.3.1., better reproducibility of results was reached by inoculation of whole tubers after injury. Usually the test is conducted after few weeks or month storage. Davila (1964) standardized storage prior testing at 5-10°C. The results correlated to field experience according to Mooi (1964) lesser than assessment of whole tubers immediately after harvest, however Lapwood (1965) found better relation with slice test. Tubers are washed, then wounded 2 mm deep with a pin frog, 4 cm in diameter (Zalewski et al. 1974) or with 16 pins distributed over an area of 12 x 12 mm (Zarzycka 2001b) or cork borer with 4 mm in diameter (Davila 1964), or 4 mm deep with a cork borer 3 mm in diameter (Toxopeus 1958), or 6 mm deep and 2 mm wide on wild potato tubers grown in greenhouse (Liu & Halterman 2009), or by falling in a drum-type sieve for two rotations (Darsow 2004/05a). Lapwood (1965) wounded tubers 6 mm deep with a cork borer, de Bruyn (1943) 5 mm, and Vowinckel (1926) cut the tuber skin on 20-30 mm^2 similarly deep in aside of eyes and hilum. A sample size of 5-6 tubers per cultivar (Lapwood 1965) or 2 x 5-10 tubers (Toxopeus 1958, Zarzycka 2001b) or 30 tubers (Darsow 2004/05a) was used. Inoculation was carried out as spraying with 10^4 zoospores (Zalewski et al. 1974) or 10^4 sporangia per ml (Davila 1964), or zoospore suspension from 5 x 10^4 sporangia per ml (Zarzycka 2001b) or 2 x 10^3 sporangia per ml (Darsow 2004/05a), or filter paper disks were placed on the wounds (Lapwood 1965), inoculum was dropped (de Bruyn 1943, Toxopeus 1958) or the tuber samples were dipped 15 seconds into suspension (Darsow 2004/05a). First 18-24 hours 14-18°C and 100% relative air humidity was adjusted followed by two weeks with 16-20°C in the dark under normal air moisture. Zalewski et al. (1974) and Darsow (2004/05a) dried the tubers superficially 18 hours after inoculation. Zarzycka (2001b) placed the tubers at 16°C in plastic trays with rose end upwards already 24 hours before inoculation; symptoms on tuber surface and the flesh on longitudinal section are evaluated. De Bruyn (1943) cut the tubers and used incubation time as criterion. Vowinckel (1926) measured the longest distance of brownish tissue to the point of inoculation in the cortex and in the pith.

A special test considering the resistance of the cortex was developed by Noll (described by Schoeber & Hoeppner 1972). Tuber skin (periderm and phelloderm) was cut; the wound was inoculated with 1,000 zoospores per ml by dropping, and then incubated at 15°C four days. Then a slice was cut one cm in parallel to the inoculated surface, which was laid with the inoculated side downwards and evaluated on the upper side for 1. the part of slices with blight symptoms and 2. the quantitative level of aerial mycelium. With 25 tubers (50 halves) he failed sufficiently to differentiate tested cultivars.

Douches et al. (2002b) injected 0.1 ml of *P. infestans* homogenate into the periderm of sterilized tubers on the apical end, incubated at 12°C and 95% relative humidity for 40 days. The quantitative degree of tuber rotting was visually estimated and completed by scanning of apical, middle and terminal slices with a flatbed scanner to determine the average reflective index. Who knows that browning of the tissue is potato clone-specific expressed and that it can be absent from other reasons will not to much expect from such method (Vowinckel 1926, Mueller 1935, Mueller & Griesinger 1942).

Interactions cultivar x inoculum density, cultivars x site of infection, cultivar x methods are described (Davila 1964, Lapwood 1965, Darsow 2004/05a). The question remains: Is assessment of wounded tubers enough representatively for defence reaction in modern potato growing? In case of damaging by falling on a drum-type sieve with two rotations before dipping in the suspension susceptibility to injury interacts with tuber blight resistance. For instance, cultivars Grata and Karlena are examples for good resistance of skin and cortex, but susceptible medulla. Both have a low susceptibility to injury. High susceptibility to injury and susceptible cortex explain the susceptible reaction of Agria (Darsow 2004/05a).

Mixed assessment with and without damaging of tubers is described too, for instance using samples of 20 tubers, 10 slightly scratched and 10 remain undamaged (Toxopeus 1958, Anonymous 1983, Bjor 1987, Lebecka et al. 2006). The difference to conditions at harvest is caused by hardened lenticels and skin, changed turgidity and changed micro organisms on skin. Mainly logistic aspects supported the decision for assessment during winter. This mix tried to consider resistance to entrance and resistance to spread of the pathogen in tuber tissue, at which last component dominates. Superficial wounding was performed by rolling the middle part of tubers over 10 nail points, 2 mm deep one day before inoculation (Bjor 1987) or by slightly scratching (Toxopeus 1958). After inoculation by spraying zoospore suspension from 5 x 10^4 sporangia per ml of a mixture of races, one ml per tuber, 4 x 10 tubers were incubated 20 hours at 15°C and 100% air moisture, then dried and continued at 15°C (Bjor 1987). Toxopeus (1958) incubated sprayed samples of 20 tubers per clone in moist peat at 10-15°C for a week; then he cut the tubers and scored 9 days later the mycelium growth 1-4. At CIP, Lima, testing for tuber blight resistance was conducted with mixed samples at 15-18°C 20 hours at highest humidity; reading followed after additional two weeks in normal humidity (Anonymous 1983). Lebecka et al. (2006) incubated the tubers at 16-18°C.

4.3.4.2. Assessment on tissue cylinders

A group of researchers used cylinders of tuber tissue to assess resistance. Langton (1972) compared inoculation of cylinders 1. with an eye and intact periderm, 2. the same wounded with a 5 mm twist drill penetrating 2.5 mm deep, and 3. cut down to medulla. 12-15 cylinders each per cultivar were inoculated, with filter paper disks on cut surface or by dropping on each eye surrounded by a ring of Vaseline or nail varnish. First variant assessed at 20°C showed insufficient cultivar differences. Variant 2 was favoured with 3,000 zoospores per ml, 4 days incubated at 10°C followed 31 days at 7.5°C and evaluating of percentage of cylinders grown through 15 mm tuber tissue downwards by the pathogen.

Jeschke (1967) used 10 cylinders cut longitudinal with a cork borer of 15 mm diameter. Cortex and vascular bundle were cut before inoculation with filter paper disk. After 5 days cylinders were cut along and after additional two days evaluated by measuring the length of necrotic area as spread of aerial mycelium from point of inoculation (mm) and the density of aerial mycelium (score). As an important advantage reduction of the personal factor in estimation of disease level was seen, but that is controverted for application in breeding (Engel 1956, Darsow 1991a) and paid with much lower number of tested clones. Dorozhkin and Kremnyova (1977) preferred cylinder of tuber tissue to assessment of whole tubers. These methods are not applied in breeding practice today.

4.3.4.3. Assessment with inoculation on the pith of the tuber

This group of methods is characterized by exclusively inoculation directly on the inner medulla (pith) or perimedullar zone of the tuber; defence by skin, cortex and vascular bundle are bypassing. Some authors used halves of tubers (Mueller & Griesinger 1942, Kostrowicka 1964, Lapwood 1965) or pieces of tubers (Jones et al. 1912, Loehnis 1922). It was learned that inoculation with aerial mycelium gives too variable results; zoospore suspension yields more reliable results (Vowinckel 1926). Rating of aerial mycelium shows the spread of the pathogen in the tissue partly better than browning (Mueller 1935); Mueller considered area of browning, area of aerial mycelium and sporulation. Schaper (1949) inoculated halves with mycelium flocks and estimated the area of aerial mycelium after seven days and the part of necrotic tissue after 10 days. Caten (1970) inoculated half tubers on one end, incubated at 18°C with 10^4 zoospores per ml and measured the longest distance of aerial mycelium at the ninth day.

Among the methods considering first of all resistance to mycelium growth in potato tissue the tuber slice test in several variants is most important (Schoeber & Schiessendoppler 1983, Swiezynski et al. 1997a). The method is suitable for large-scale testing because of quick and simple execution, weekly rhythm, low number of tubers necessary, low weight which is to handle, small room is necessary, disease is sure to establish, and results are relative good reproducible. Already Hecke (1898) worked with tuber slices. Koeck (1931) incubated 0.5 cm thick slices in Petri dishes, inoculated with mycelium flocks and observed speed of mycelial growing and density of aerial mycelium on slice surface. Lehmann (1938a) changed the method by inoculating suspension of zoospores between two slices which reduced rot caused by other pathogens. The scale 1-5 considered the possible range of browning and development of aerial mycelium including its compactness. He noticed different quantitative pathogenicity. Rudorf and Schaper (1951) and Weindlmayr (1962) reduced the temperature to 18-20°C.

Most users relate to Lapwood (1965), who cut two slices per tuber, 11 mm thick from six tubers per clone and inoculated by filter paper disks soaked with zoospore suspension. Two days later the slices were turned over. Area and density of aerial mycelium were scored on the fourth to eighth day after inoculation on the surface in opposite to the inoculated one. Central inoculation was recommended in comparison with inoculation of cortex. Oertel (1972) adapted the slice test to pre-breeding for blight resistance to assess field-grown tubers. Five tubers per clone were sufficiently first year without replication, the following years with two replications. Area of aerial mycelium and its density were scored 1-9 about 96 and 168 hours after inoculation. Whilst results of BC2- and BC3-material of different years well correlated, cultivars did not so. Darsow (1987a) considered three years assessment from three different growing sites necessary for variety candidates. Standardized pre-storage and inoculation with a mix of three isolates by means of filter paper disks and incubation at 17-19°C were applied. Colon et al. (2004d) recommended 2 x 6 tubers with two slices each to inoculate with 5 x 10^4 zoospores or 15 x 10^3 sporangia per ml and incubated at 16-18°C. The percentage of colonised slice area is estimated after 7-10 days. Recommended standard cultivars were Eersteling and Gloria (early), Bintje and Escort (second early), Alpha and Robijn (late). Flier et al. (2001a) dropped 2 x 10 slices with a single 10 µl droplet with suspension from 2 x 10^4 sporangia and estimated after eight days at 15°C the area of necrotic tissue (%, transformed to square root) and of mycelium coverage (score 0-9 transformed to ^{10}log). Both traits were used by Andreu et al. (2010) in the same manner.

The changes including Polish experience described Zarzycka (2001b). Double slices, each 10 mm thick, are cut out from middle part of the tuber. 1-2 x 3-10 double slices per clone are inoculated by dropping a zoospore/sporangia suspension from 5 x 10^4 sporangia per ml between the connected double slices and then placed in glass covered plastic trays at 16°C in dark. The area covered with mycelium and the sporulation intensity is estimated in a 1-9 scale on the outsides of the slices. One or two replications are used.

Schoeber and Hoeppner (1972) varied the test by incubation of slices at 15°C and waiting 24 hours for wound healing before dropping with 1,000 zoospores per ml, 50 µl central per slice. The 4 x 20 slices per clone were observed 3-9 days after inoculation and scored 1-5; the total sum of six observation dates is then transferred to a 1-9 scale. Erjefält (1975) worked similarly, but inoculated with filter paper disks soaked in suspension from 50 sporangia per mm^3 and scored aerial mycelium after 6, 8, 11 and 13 days at 17°C; the resistance is calculated as an index. Deahl et al. (1974) applied slices according to Lapwood, but after 24-48 hours of wound periderm formation at 20°C zoospore suspension from 10^4 sporangia per ml was dropped. Scoring of necrotic part followed after vertical cutting of the tissue 96 hours after inoculation. Schoeber and Schiessendoppler (1983) recommended 2-3 years assessment for describing of cultivars and selection in breeding applying the slice test with wound healing. A practical reason for wound healing is reduction of overgrowth of *P. infestans* by *Erwinia* sp. or *Fusarium* sp. (Noll 1968). Is the reaction after wound healing representatively for reaction in the field?

New is to record affected tuber tissue by a digital image analysis technique which results in an average reflective intensity between 0 and 100 related to control (Niemira et al. 1999, Kirk et al. 2009, 2010). Each tuber is measured in the apical, middle and basal region. This method saves manpower, but has additional risk of wrong decision concerning severity of late blight attack from other reasons of browning or clone-specific suppressed or delayed browning or effects of tuber flesh colour.

Also in applying tuber slice test the physiological stage of tubers is to consider. First 2-3 weeks after harvest and the period of sprouting are to avoid because of changed reaction (Malcolmson 1976/77, Bhatia & Young 1985, Darsow 1987a, 1988a, Swiezynski et al. 1997a).

Inoculation by a sub-peridermal injection with a hypodermic syringe and needle at the apical end of the tuber is another method using controlled injury of tuber. About one cm from the dominant sprout 10 tubers per sample were injected to a depth of one cm (Douches et al. 2002b).

4.3.5. Assessment of tuber blight resistance using ELISA or PCR

Resistance to colonisation or spread of *P. infestans* in potato tuber tissue measured as lesion growth rate may be assessed by ELISA too (Beckman et al. 1994, Knapova 1995). More methodical development is necessary before application in breeding for resistance is expected (Schoeber-Butin et al. 1995). A quantitative PCR has been developed to assess the growth of *P. infestans* in resistant and susceptible tomato (Judelson & Tooley 2000).

4.3.6. Indirect assessment of tuber blight resistance using electrolyte leakage

Even a test is published based on measuring of electrolyte leakage of tubers grown in vitro for screening tuber tissue with *P. infestans* culture filtrate (Cristinzio & Testa 1999). Six tuber disks were placed in 20 ml of 15% culture filtrate and in hourly intervals its conductance was measured in comparison to control.

4.3.7. Components of tuber resistance

4.3.7.1. Resistance to entrance

Resistance to entrance/beginning of spread is considered by assessment of undamaged whole tubers or parts of it with inoculation of intact tuber skin (see 2.8. and 4.3.-4.3.3.2.). Practical application in large scale is known at SCRI Dundee, Scotland (Stewart et al. 1983b), JKI Gross Luesewitz, Germany (Darsow 2004/05a) and Danish Potato Breeding Foundation Vandel, Denmark. High environmental effects cause high variability and require several tests with many tubers. More research is necessary.

Mainly percentage of infected tubers is used as criterion of resistance (Mooi 1964, Stewart et al. 1983b, Gans & Wooster 1987). Flier et al. (1998) stated the average percentages of infected tubers, transformed the data according to Gregory (1948) and interpreted the transformed data as a relative measurement of infection efficiency (IE). Lapwood (1967) recommended the weighted part of invaded tuber tissue.

4.3.7.2. Resistance to mycelial spread

Growing of mycelium in tuber tissue can visually not directly exactly be observed, the pathogen has invaded more tissue than shows necrotic change or sporangiophores. Tissue colonisation may visually be estimated by area of browning or/and area covered with aerial mycelium. Mueller (cited by Vowinckel 1926) and Lapwood (1965) regarded browning of tissue in half and whole tubers as unsuitable measure of tissue colonization because cultivars differ in intensity and course of time; cultivar-specific reaction in relation of both are confirmed by Haenni (1949) and Huettenbach (1951). The relation of browning and aerial mycelium is influenced by temperature during the test (Mueller and Griesinger 1942). Additionally, cortex and medulla often reacts differently, and isolates may cause different expression of browning or aerial mycelium. Therefore Oertel (1972) decided to consider only the worst expression of both on each slice, respectively, for clone evaluation; Pietkiewicz (1976) recommended using only aerial mycelium on tuber slices as measure of resistance of tuber flesh.

So far as resistance of tubers has been assessed variants of tuber slice test are mainly used. However, most methods include processes of penetration and establishment of disease into the time which is related to mycelium growth. The differences may be caused up to the establishment and not by different speed of mycelium growth (Clarke and Kassim 1977). Measuring in mm has no advantage to visual estimation in % or scores according to our results (Darsow 1991a), but requires about five times more time.

4.3.7.3. Generation interval

Vowinckel (1926) discussed the practical advance of generation interval which may vary up to several days. In practical breeding this component requires repeated observation in at least six hours interval and is not applied. In research Piotrowski et al. (1973) considered this component too. However, in tuber tissue differences in sporulation should be of much lower epidemiological effect than on leaves. Therefore cultivar-specific generation interval is not of interest for selection in breeding.

4.3.7.4. Combining of components and its correlations

In assessment of whole tubers resistance to entrance and resistance to spread of mycelium within the tubers, both is considered by calculation of an index from the number of infected tubers in nine classes of disease severity weighted according to the date of observation (Darsow 1983a, 2004/05a). Osipova and Ligay (1978) calculated an index from percentage tubers with superficial symptoms and depth of mycelium penetration into the tuber. Flier et al. (1998) calculated a tuber blight index (TI) as $TI = -\log_e (IE \times SI)$, in which IE means infection efficiency and SI the disease severity estimated in average of 10 cut tubers. Lapwood (1967) recommended only considering the weighted part of invaded tuber tissue.

The components as lesion size, sporulation intensity and generation period deriving from tuber slice test correlated with each other ≥ 0.94 (Piotrowski et al. 1973). The data of three consecutive years correlated for the components similarly r = 0.66-0.78, as well as to foliage blight resistance r = 0.47-0.49. Pietkiewicz (1977) found in comparison of whole tuber test of 36 cultivars grown in greenhouse, cold frame and field lower correlations (r = 0.49-0.89) than between years (r = 0.61-0.90) and test date in the same year (r = 0.81-0.88). Resistance to spread and resistance to infection correlated with r = 0.62 (Pietkiewicz 1976).

Own methodical experiments led to long-term use of three laboratory methods in selection of pre-breeding material for late blight resistance, which react to different components of resistance and complement each other. Yearly suitable results for selection were achieved, middle level of resistance required 2-3 years average for decision (chapter 4.4.).

4.4. Methods of assessment of tuber blight resistance at ZL Gross Luesewitz

4.4.1. Test of small, greenhouse-grown tubers at ZL Gross Luesewitz

This is the first step of assessment and selection of tubers for blight resistance, applied to all seedlings in pre-breeding for blight resistance and for evaluation of wild and cultivated species of gene bank GLKS Gross Luesewitz since 1967 (Oertel 1972, Darsow 1988b, Darsow 2000b). During harvest in greenhouse after discarding of seedling plants because of eye depth, length of stolones and other deficiencies tubers of each remained pot are completely put in a paper bag, marked and stored at 4-6°C up to December. Then the biggest tuber is separated for planting and up to four tubers are prepared for testing for resistance to *P. infestans*. They are put into test boxes in kind of string of pearls between plastic sticks. A second person records clone number, number of tubers and position in the box. Immediately before dipping into suspension, a section of 2-5 mm is cut from the heel-end of small tubers, in case of bigger tubers from heel- and rose-end (Darsow 1992a, fig. 32). According to expected level of resistance suspension is adjusted to 7-20 x 10^3 sporangia ml^{-1} and then given two to three hours in refrigerator. Nearly 100 tubers are dipped successively into the same suspension, and then new 300 ml are taken. The pathogen can penetrate the tuber *via* eyes, lenticels, hilum or wounds in this seedlings test. Air humidity of 95-100% in the beginning, about 80-90% next days and 95-100% on the sixth day are regulated by moist filter paper at 16-18°C. Figure 33 shows a cut-out of tubers in the moment of estimation of blight seven days after inoculation. As well area and density of aerial mycelium on cut surface, eyes and lenticels are visually estimated (fig. 34) as browning of tuber tissue superficially and after cutting in longitudinal direction (fig. 35). Score 9 means no symptoms, score 1 95-100% invaded tissue. Aerial mycelium is scored according to the scale given for slice test. Browning score 8 and 7 mean necroses sharply separated from healthy tissue, score 6 corresponds with limited browning of 5-6 mm below the cut or other points of entrance. Score 4 and below 4 is passed for too susceptible in pre-breeding (Fig. 35). Tubers with not sharp browning of 25-30% of the cut area or without browning combined with aerial mycelium ≤6 are scored 5 for browning of tissue and not better. High variability of tuber size requires adapting of the scale.

Tubers of a standard population are tested for comparison on each date of inoculation. Long time eye cuttings from field-grown tubers of cross parents were cultivated in parallel and used for comparison of parents with its progeny. Very clean culture on tuber slices proved cultivars reduces soft rot. Overgrowing of cut surfaces by *Rhizoctonia solani* disturbs scoring of blight symptoms.

This test reduces the number of seedlings additionally to 40-60%. By this seedlings assessment two third of the clones are eliminated in the very early stage, which are proved to be too susceptible on tubers according to tuber slice test in following years. However, about 14% of clones resistant in the tuber slice test, are false eliminated by selection according to the small tuber assay of seedlings (Darsow 1988b, Darsow 1992b). It follows from tissue-specific resistance and genotype-environment interaction (Darsow 2005a, b). On material of backcross four and five negative correlation of tuber blight resistance with other traits was not detected, but remained seedlings were in all tests for foliage and tuber blight in average significant more resistant than rejected ones. In pre-breeding such result is good from economical point of view and realizes very high priority of blight resistance among the many traits in selection. But the risk of error increases with decreasing level of resistance. About 120 person-days are necessary to assess 8,000 seedlings (Darsow 1992b).

Up to now about 2,550 accessions of 119 tuber-bearing species of the gene bank Gross Luesewitz (GLKS, belonging to IPK Gatersleben) are tested with about 210,000 small tubers (Darsow 2000a, Darsow et al. 2002).

4.4.2. Tuber slice test at ZL Gross Luesewitz

This method reflects defence of wounded tuber tissue without wound healing (Darsow, 1987a). Samples with four healthy tubers of middle size without injury and viridescence are taken two to three weeks after harvest. From A- to D-clones two samples are taken, from single-hill-plants one sample. After storage at 6-8°C tuber slice test is carried out from beginning of November to the end of year. One week before starting assessment of breeding material a pre-test is conducted on standard cultivars/clones with different inoculum densities and according to their reaction the inoculum density is adapted to the season-specific predisposition. Crossways to the longitudinal axis two slices of 11 mm thickness per tuber are cut and put in described test boxes. Generally two densities of inoculum from three isolates with virulence genes 1-11 are applied in parallel, each on one of the both slices of the same tuber; density relation is 10^4 and 2,5 x 10^3 sporangia ml^{-1}. Slices are inoculated by one drop of 10µ on the centre two to four ours after cutting. Then slices are incubated on 16-18°C and 95-75% air humidity most days, 100% during first and last 14 hours. Darkness is favourable. Slices are turned over after 20 hours and are estimated 138-143 hours past inoculation. Both, superficial and by cutting visible browning of slice tissue and the area and density of aerial mycelium are rated (table 18, fig. 36). Minimal aerial mycelium can only be detected in light at an oblique angle. In case of score 9 for aerial mycelium, which is usually estimated only on the not inoculated surface, the underside is obtained too. Some clones show nearly no browning, but intense aerial mycelium. In that case score 5 is given for browning. Flat dilatation and type of browning are considered. At scores eight to six necroses are dark brown, sharply delimitated from healthy tissue and dry. On the contrary, scores 4-1 are characterized by flowing change from invaded brownish, partly soft part to healthy tissue. Tuber blight resistance is calculated from average of scores for browning and aerial mycelium.

Table 18 Scale for estimation of attack in tuber slice test (% of covered area of a middle sized slice).

Score	9	8	7	6	5	4	3	2	1
Aerial mycelium	0	0.5%	4%	12%	36%	55%	75%	87%	100%
Browning of tissue	0	4 mm	12mm	15%	25%	45%	67%	83%	100%

In table 18 the percentage refers to tubers of middle size. In breeding material a variation in tuber size is without fail, therefore operative adaptation of the scale is necessary. Because of tissue-specific difference, for instance between medulla and cortex, a scale with fixed mm is not more correctly.

The second samples of tubers from A- to D-clones are tested at an interval of two to three weeks as second replication. So results are present of two different dates with different inoculum densities each from four slices each. Resistance of the clones of each test date per year is calculated uniformly in following variants:

1. average of both dates and of both densities (general average per clone),
2. average of both dates with high density only,
3. average of both dates with low density only,
4. average of only one date and both densities,
5. average of only one density of one date.

Best differentiation of the breeding material and simultaneously resistance level of standards nearest to their expected values are criteria of decision for tested material at the same date. Standard clones (cultivars) of each maturity group are included on each test date. The test of isolates on differentials has been done no longer than three month before. In table 5 the tuber slice test with 4 x 4 slices had the best differentiation of varieties with a LSD of 2.2 scores and 81 significant differences as well as best reproducibility over the years with a mean standard deviation of 0.6 scores (Darsow 2004/ 05a). With 8 slices clonal differences of 1.1-1.7 scores were significant; two replications reduced the critical difference to a half. One-year negative selection is shown to be dangerous, only one clone in six was in all seven years tested correctly remained, five other were wrongly rejected due to clone/year-interaction in at least one year (Darsow 1987a). About 56% of tested clones mean values comparisons were found to be significant, the relation of standard deviations in test for resistance to *Phytophthora*: *Fusarium*: *Erwinia* was 1:2:3 (Darsow 1978).

The part of environmental variance is lower than in whole tuber test (Darsow 1987a, 2004/05a). Comparison of results of different years showed often correlation coefficients near r = 0.6.

4.4.3. Test of freshly harvested whole tubers without visible injury for resistance to *P. infestans* at ZL Gross Luesewitz

This test in laboratory most representatively considers conditions and factors of tuber infection in the field. The cortex as natural barrier is assessed (Darsow 1983a). Since inoculation occurres on day of harvest or on next day, six plants per clone are grown only for this assessment.

The location Gross Luesewitz is characterized by 605 mm rain a year, a medium daily temperature of 7.8 °C, diluvial sandy loam of classes D3 and D4. Fertilization of 80 kg N, 140 kg P_2O_5 and 200 kg K_2O/ha was given. The tubers were planted in all trails in rows 75 cm wide and with

a distance of 28 cm in the drill. Against weeds pre-emergence herbicides are applied, virus infections are reduced by insecticides according to advices of plant protection service. Haulm is maintained without blight by contact fungicides. The number of clones and its range of maturity influence the necessary number of groups respective harvest dates to delimit differences in firmness of skin. Pre-breeding material up to now has been divided in two groups; the material was separated near the middle of second early. In cultivar testing three groups are recommended: very early and early, second early, second late and late (Darsow 2003a). All B-, C- and D-clones (third to fifth year in the field) are tested. Harvest follows about 8-10 days after haulm killing near August 10 and 25, respectively. Six days old culture of *P. infestans* on slices of old tubers has to be available in large amount to that date.

During harvest injuries of skin have to be avoided, we use a shaker digger driven with low number of rotations per minute. Tubers are harvested in the morning, collected into net bags and washed in it by hand, if necessary. Washing of tubers before inoculation depends from level of pollution by soil and has to be decided for all clones or none because of its influence on quantitative resistance level (Clulow et al. 1995). Subsequently visibly damaged, sick or green tubers are eliminated and two samples of 30 intact tubers per potato clone and replication were placed in a wide-mesh plastic bag each. Mostly inoculation by dipping in suspension on day of harvest was not possible, so the next day zoospore suspension from 300-500 sporangia/ml and 1,000-1,200 sporangia/ml in parallel is prepared, each for one of the both samples per clone and replication. Use of two different inoculum densities proved to be much better than two replications. However for national assessment of cultivar candidates two densities and two to three replications are recommended. As in all other tests mix of three isolates with high aggressiveness (unspecific pathogenicity) and maximal combination of virulence are used. Tubers in net bags are briefly dipped in about six litre suspension per 10-litre-bucket (fig. 37). Each ten samples new suspension is used. After drain off excess of inoculum the tubers are incubated in large, closed plastic bags at 16–18 °C and 100 % air humidity during 15–18 h. Thereafter the samples are incubated in open plastic trays at 16–17 °C, low moisture and darkness. As well careful wipe dry of tubers before putting into the plastic trays and of trays at first date of observation as limiting temperature to maximal 18°C avoid wet rotting (Darsow 1983a).

The intensity of single tuber attack is scored externally on a scale of 1-9 for 0, 0.5, 4, 12, 25, 50, 67, 80, and >95%, respectively, in which 1 means no symptoms, and score 9 95-100% rotten tissue of a tuber, first time after eight days. Tubers with score one and two remain in the tray. Attack with score 3 and stronger is estimated considering tuber surface and surface of cut of each tuber. The external scoring is corrected according internal symptoms (reduced, when limited to the skin; increased, if medulla was long-ranging attacked). The score is listed and the tuber is discarded. The second evaluation followed 12 days after inoculation (fig. 38) with the same procedure. A third evaluation after about 30 days includes all remained tubers and applied the full range of the scale 1-9 (fig. 39). An index is calculated by the number of attacked tubers times intensity of pathogen growth into the tuber tissue (score) for each date of observation. In the following manner the sum is calculated for the first and second date: (number of tubers x score 3) + (number of tubers x score 4) + (number x score 5) + (number x 6) + (number x 7) + … (number x 9). The sum of the first observation is doubled. This step increases the differentiation between highly susceptible clones and the middle group. An index of resistance is calculated: BFR = (Sum for fist date) x 2 + sum for second and third date. BFR of samples with lower number of tested tubers than 30 has to be corrected to the basic number 30. BFR is transferred into scale 1-9, in which one means highest level of susceptibility. Score 1 is fixed for the highest level of attack in the experiment and in consideration of reaction of (very) susceptible standard cultivars. The general sum BFR was then non-linear transformed to the scale 9-1 as shown in table 19. Subdivision considers classes of tenth of full scores. The scale is yearly adapted to the range of results, for instance to a longer (sum 0-630) or shorter range (sum 0-300).

Table 19 Conversion of index into scores 9-1 of tuber blight resistance in assessment of freshly harvested whole tubers – table for a test collection up to index 415 as highest susceptibility (score 1).

Index	30	40	50-51	65-67	80-83	130-34	183-88	239-44	300-08	378-85
Score	9	8.5	8.0	7.5	7.0	6.0	5.0	4.0	3.0	2.0

Infections occur *via* eyes (Fig. 5), lenticels (Fig. 4), wounds or hilum (fig. 6), in some cases all different ways of entrance may be found on the same tuber. Two inoculum densities allow better to adapt to seasonal conditions by using the average of both samples or of only one. Resistance may affect on number of infected tubers and/or progress of rotting (growth rate of mycelium, compare fig. 2 and fig. 7).

The cultivars Eersteling, Gloria, Karlena, Marabel, Tomensa, and two clones of ZL are very early to second early standards. Bintje, Maxilla, Cara, Kuras und three clones of ZL are used as standard cultivars for second early to late material. Selection was based on results of at least two years average. Growing in two different environmental conditions would be better than only one location.

4.5. Methods of quality assessment, importance of the traits and its inheritance

4.5.1. Resistance against blue bruise

Mechanical damage is a major concern for potato production and potato breeding. More than only external and internal damage can be distinguished; the Washington State University classification system described six different bruise types, in which blue bruise is one (Storey 2007). In this mechanical load and/or physiological deterioration causes discolouration of tissue due to loss of membrane function to separate compartments of cells, which results in development of melanin. Susceptible clones show grey, blue or black tuber parts (patches of the flesh), which become visible only after peeling. That damage seems mainly to occur during loading, unloading, grading and packaging (Molema et al. 2000). Low frequency of blue bruise leads to more wastage; frequent occurrence excludes utilization for table potato and processing. Higher discolouration at the stolon end and the narrow sides of tuber is explained by closer position of lignified xylem and tracheids to tuber surface (Croy et al. 1998). Two components may be distinguished, the bruise threshold (energy impact at which tuber begins to bruise) and bruise resistance (bruise volume). Genotypic resistance to damage is involved in this trait, which is very complex (van Eck 2007).

A sample of 10-20 uninjured tubers per clone was taken about two to three weeks after harvest and one to two month stored at 4°C. Directly from cold storage tubers are put in a box of a device, which carried out an up and down-motion and pushed tubers against gravity for 45 seconds. Thereafter tubers were exposed about 48 hours to 17-20°C, were then peeled and up to two and a half hour later estimated according to the percentage of surface discoloured (table 20).

Table 20 Scale for scoring of blue bruise

Score of resistance	9	8	7	6	5	4	3	2	1
Part of blue bruise (%)	0	2	6	13	28	55	70	85	100

Examples of four intensities of blue bruise are presented in figure 40. Some clones discoloured light grey, other black. Flesh colour varies visual impression of the same percentage of blue bruise. Reference samples help to ensure constant measure during scoring 1-9. Simple cutting instead of peeling of tubers resulted in better scoring and lesser differentiation. Additionally the intensity of external damage as shatter or cracking is scored, registered and considered in selection of clones. Avoidance of such rough mechanical damage is according to Howard (1982) more a task for agricultural engineers in designing better machinery rather than for breeders in developing resistant cultivars. GCA is the main component of genetic variance (Bradshaw & Mackay 1994).

4.5.2. Suitability for crisps

The main factor of suitability for crisps and French fries is the genotypic expression of the Maillard reaction (Haase 2007, Haase et al. 2007). Excessive browning and development of off-flavours results from reaction between reducing sugars and free amino acids at high temperatures. The Maillard reaction is not a single reaction, but a complex pathway with forming of melanoidins in the final stage (Haase 2007). The concentration of reducing sugars is the crucial determinant, which depends on genotype and storage conditions, mainly storage temperature, and should not be greater than 1.5 g kg^{-1} fresh weight with more than 22% dry matter (Schuhmann 1999). Cold storage at 4°C saves application of sprout suppressants, but increases the reducing sugar content, known as cold-sweetening, in which many gene loci are involved (van Eck 2007). Dale and Mackay (1994) assumed that recessive factors are involved in low-temperature stability. The reducing sugars are the key component for formation of acrylamide which are known to be potentially carcinogenic in backed potato products (Hebeisen et al. 2005). Two candidate genes and their products have been shown to play a major role in regulating the formation of reducing sugars in tubers: UGPase and VAcInv (Sowkinos 2007). The glucose content (one reducing sugar) is inherited in a polygenic way. Transgressive individuals and maternal effect were found. Both, additive effects (GCA) and genetic interactions (SCA) are involved in determining glucose content in tubers stored at 6°C (Jakuczun & Zimnoch-Guzowska 2004). The colour of crisps or French fries correlates well with the acrylamide content and is used as indicator for selection (Hebeisen et al. 2005, Juergens & Darsow 2005).

In our pre-breeding this trait is assessed in a special assessment with two to three persons directly from cold storage after 3-4 month at 4°C. A sample of four medium-sized tubers per clone is washed; three slices per tuber are planed, 1.2-1.3 mm thick. Slices are rinsed with running water, wiped, put into 180°C hot vegetable fat and backed so long, till the light point in the centre of the slices disappears. Then crisps are taken out of fat, drip off, and put on plate. Defects as bubbles and wrinkles are recorded. Discolouration due to backing is scored in following manner: score 1: black, 2: dark brown, 3: spotted brown, 4: spotted non-uniform grey brown, 5: slight brown, non-uniform, spotted, 6: slight non-uniform light-brown, 7: mainly uniform yellow, 8: clone-typical uniform light, 9: bright, spotless light. Reference samples help to ensure constant measure during scoring 1-9. Surface should be sleek, taste good, consistency firm (Weber & Putz 2003). Score ≥7 means suitable. Figure 41 gives an example for crisp colour in scores 3, 4, 5, 6.5, 8 and 8.5 in the 1-9 scale.

For quality of crisps and French fries not only dry matter content is important but also the distribution of dry matter in the tuber. The pith usually has reduced starch content, but the size

and shape of pith and the difference of starch content between perimedullar zone and inner medulla or pith strongly depend on genotype and causes quality differences (van Eck 2007). Watery pith results in reduced quality of crisps and of French fries. Breeding progress over more than 100 years is calculated per year: defect-free chips increased 0.23%, chip colour increased 0.15-0.18 agtron units, reducing sugars decreased 0.0013-0.0031% of fresh weight (Love et al. 1998).

4.5.3. Suitability for French fries

It is expected if tuber dry matter ranges between 19 and 23% and reducing sugar concentration below 2.5 g kg^{-1} fresh tuber weight (Schuhmann 1999). The same reaction as described in 4.5.2. is important for French fries. Our testing was carried out in February after about 3-4 month cold storage at 4°C. A sample of four medium-sized tubers per clone is washed, rose- and heel-end are cut and taken away, and rods of 10x10 mm are cut in parallel to longitudinal axis of tuber with a cutting machine for French fries. Rods are rinsed with running water (fig. 42), wiped, and blanched five minutes at 90°C in water (fig. 43). Sample is fried after drip off for three minutes in 180°C hot vegetable fat (fig. 44). Frying is repeated for two minutes after cooling down. Then colour is estimated of all samples and shape, smell and taste of best samples are assessed. Discolouration of French fries due to frying is scored 1-9 considering experience in Karlsruhe:

1. completely dark brown, edges black,
2. strong one-sided discoloured, edges predominantly black, very irregularly,
3. one-sided discoloured, edges black-brown, very irregularly,
4. strong grey, brown or glassy, predominantly irregularly, edges mostly dark-brown,
5. brown or dull, pale, glassy, streaky, edges brown,
6. slightly brown, slightly glassy, edges mostly darker,
7. yellow-yellowish brown, reddish yellow, predominantly uniform, slightly darker edges,
8. deep yellow, uniform,
9. bright golden, uniform.

Reference samples help to ensure constant measure during scoring 1-9. French fries should not be changed in its shape, their smell and taste should not be objectionable. They should be outside crunchy, inside floury-dry to slightly moist-juicy. These traits are registered for best samples (score ≥7). The influence of some factors on French fry colour is analysed by Burke et al. (2005). Four QTL are found which contribute to light colour (Douches & Freyre 1994).

4.5.4. Suitability for table potato

Assessment of table potato index is carried out between November and February on samples taken a day before from cold store by cooking done of peeled medium-sized tubers, which are obviously healthy, undamaged and not green, in water about 20-30 minutes. Six samples with 5-6 tubers each are boiled at the same time and then five traits are estimated concealed by a panel of 3-4 persons with scores 1-5, up to noon 24 samples. Each sample with five tubers on a plate is firstly scored for its appearance after cooking: (5: very well, evenly coloured, not glassy, not discoloured; 4: good, nearly equable constitution, some irregular colour, not glassy, may be burst; 3: sufficiently, irregular colour of tuber tissue, a bit discoloured, a bit cooked to rags; 2: not sufficient, unbalanced constitution, irregular colour of tuber tissue, middle strong discolouration after cooking, intense cooked to rags, not to moist; 1: bad, deep discoloured, mushy).

Texture of cooked potato could be a generic term for disintegration, consistency, mealiness and cooking type. Composition of cell wall, of middle lamellae and gelatinization of starch has been studied in relation to texture, which seems under polygenic control (Dale & Mackay 1994, van Eck 2007). It is observed that pectic polysaccharides of mealy clones contain more and/or longer side chains than non-mealy clones, which had more branched and a higher amount of branched pectic polysaccharides (van Marle et al. 1997a). Already elder literature points to correlations between disintegration, mealiness and consistency (Vogel 1962). Although texture depends to some extent on environmental factors, it is well established that genotype plays the most important role in determining texture. In cultivar breeding it is usually not difficult to discard clones which are obviously either too mealy or to waxy: the difficulties are in selecting for the usually required degree of slight mealiness (Howard 1982). This type shows the highest environmental influence and means therefore highest challenge for combination with polygenes for resistance to *P. infestans*.

In pre-breeding at Gross Luesewitz a well-tried procedure of estimation of traits is continued as described in following (developed by J. Vogel before 1990): After estimation of appearance each tester takes a tuber on his plate and estimates the degree of disintegration on cooking: (5: smooth surface, 4: slightly be burst, 3: strongly be burst, surface middle cooked to rags, 2: shape of tuber till perceptible, 1: tuber completely cooked to rags).

The consistency of cooked tuber describes tissue firmness after cooking and is ascertained by pricking a fork in the tuber (fig. 45, score 5: uniform firm, 4: little firm, 3: not firm, 2: soft, 1: mellow surface and very firm pith). The consistency seems very independent from other components of table quality (van Marle et al. 1997b).

Taste on the tongue and appearance decide the degree of mealiness (5: not mealy, 4: a bit mealy, 3: mealy, 2: rather mealy, 1: very mealy). Taste is according to Howard (1982) the most difficult character of cooked potato quality. Organoleptic test leads to individual scoring of the taste of a clone by eating of a tuber part (5: very well taste, true to type, balanced, mildly, not very wet, not very dry; 4: typical potato taste, good; 3: true to type, slightly peculiar flavour, slightly sweet or very dry, is not a nuisance to a meal; 2: strange or tasteless, sweet, bitter, wet, tart; 1: repulsively or distasteful, fusty, bad). Taste is neutralized between two samples with white bread and mineral water. It is assumed that elimination of clones with taste below score three at the same time effects as negative selection against high glycoalkaloid content, which is not generally tested.

Two additional parameters are calculated, cooking type and index of table potato quality. The cooking type characterizes clone-specific behaviour during cooking and is derived from sum of (score for disintegration x 100) + (score for consistency x 100) + (score for mealiness x 100). Sums below 940 mean cooking type D (intensely cooking to rags), indices of 940-1079 describe cooking type C (mealy, bursting), 1080-1149 cooking type B/C (a little bursting, still mealy), 1150-1219 cooking type B (transitional type to firm cooking), >1220 cooking type A, firm cooking, not bursting, not mealy. The starch content plays a role in it. As second calculation, index of table potato quality, marks suitability of cooked potatoes for domestic use. It considers after cooking appearance, discolouration and taste. Score for appearance is multiplied with 100, score of taste with 150 and score of discolouration with 40, results are added. We prefer to transfer indices to the 1-9-scale in following manner (table 21). Score nine means the very best expression. Tenth part of scores is considered by interpolating.

Table 21 Shorted version of table to convert index of table potato quality 265-1485 into scores 1-9

Index	<330	540-54	675-87	800-09	900-09	1000-12	1285-1304	1285-1304	>1460
Score	1	2	3	4	5	6	7	8	9

Discolouration of row tuber tissue is a nuisance to processing and table purpose. It considers the process in which phenolic compounds are oxidized by the enzyme polyphenol oxidase (PPO) to quinones and the quinones transformed to dark pigments (Friedman 1997). The level of phenolic compounds, the activity of PPO and the level of free amino acids including tyrosine are found to be involved in this discolouration. A gene family of at least six genes regulates the PPO activity (van Eck 2007). Usually discolouration after peeling of tubers is prevented by use of chemicals as sulfiting agents – an undesirable additive to human food. Nevertheless, progress in breeding happened. In pre-breeding row tuber tissue discolouration occurs with different intensity to grey or black after core out of two cylinder bores in parallel to long axis of a tuber with a cork-drill. Four tubers per clone are assessed in January, and stored on air in room temperature. Discolouration is visually estimated after five and 18-24 hours under 80-90% atmospheric humidity. At the beginning reference samples for score eight (very little discoloured) to score one (black) are chosen, for instance as in figure 46. The average of both intervals of observation is used to characterize the trait in the 1-9 scale.

Discolouration after cooking is assessed before complex assessment of table quality as separate examination. This discolouration is considered as one of the key quality defects for fresh consumption and processing (Wang-Pruski 2007). After cooking a bluish-grey haze in different intensity can be observed when potato tissue is exposed to air. Chemically, in first step a colourless reduced ferrous ion-chlorogenic acid complex is developed, which is then non-enzymatically oxidized to a dark ferric complex following exposure to oxygen in the air (Friedman 1997). The severity of darkening depends on the ratio of chlorogenic acid to citric acid concentrations in the potato tubers, which is genetically controlled and influenced by environmental conditions (Wang-Pruski & Novak 2004). Additionally genes of the anthocyanin biosynthesis pathway may be involved (De Koeyer et al. 2010). This trait does not affect the flavour or nutritional value; it affects the appearance of the tubers. The degree of darkness is always higher at the stem end and in the cortex. Season, location of growing and storage conditions interact to some degree with predominantly genetic effects (Wang-Pruski 2007). In cultivar breeding relative high heritability is mentioned by Howard (1982), whilst in pre-breeding this trait proved to be more difficult and more confirming inheritance in a polygenic manner (Dale & Mackay 1994). Four major QTL are detected on chromosomes II, IV, VI and X, additional minor QTL's (De Koeyer et al. 2010). Veerman (2001) found on cultivar level 32-40% of the total variance caused by potato clone, 26-35% by year, 14-16% by in-plot variation, 4-5% by location, and 5% by triple interaction. GCA and SCA take part in inheritance (Bradshaw & Mackay 1994).

To assess genotypic reaction of pre-breeding material four medium-sized tubers per clone, which are obviously healthy, undamaged and not green, are cooked done, are hot peeled, longitudinal cut, put with cutting surface on a plate. Discolouration is estimated after 5 and 15-20 hours, average of both scores is used. Reference samples help to ensure constant measure during scoring 1-9.

Colour of tuber flesh plays a part in respect to preference of different colours in different countries or regions for fresh market. Pre-breeding material is scored after harvest according to following key with colour and (score): white (1), white to yellowish white (2), yellowish white (3), yellowish white to bright yellow (4), bright yellow (5), bright yellow to yellow (6), yellow (7), yellow to deep yellow (8), and deep yellow (9). Other tuber flesh colours were directly recorded.

Our pre-breeding is open for any colour of tuber flesh, but considers regional preferences. Yellow flesh is preferred and its high broad sense heritability leads to good corresponding results of different years and simple selection. Yellow is dominantly to white and is determined by a single gene but there are in addition modifying genes for different degrees of yellowness (Howard 1982). Schick & Hopfe (1962) assumed several dominant genes to be responsible for different intensive yellow. Meanwhile is known that among 11 beta-carotene-hydrolase-2 alleles only one has a major effect, changing white into yellow flesh. None of the involved lycopene-epsilon-cyclase alleles have a large effect. A determined homozygous recessive zeaxanthin epoxidase (ZEP) allele combined with the dominant beta-carotene-hydrolase-2 (CHY2) allele expresses orange tuber flesh (score 8-9, Wolters et al. 2010). It takes several generations to get clones with score 5-6 after starting with a highly blight resistant wild clone of white flesh and crossing with a cultivar characterised by score four or five because of advantages in other traits compared with a deep yellow one.

4.5.5. Starch content

A variation of starch content between 8% and 33% is known (Yashina et al. 1973, Haase 2000). Starch is the major component of the dry matter content of potato tubers, accounting for approximately 70% of the total solids. High starch content and high yield of starch per ha are desired for special purposes of food and general for non-food starch production. It is determined indirectly by the difference between the weight of a tuber sample in air and the weight by the same sample in water with the under-water weighing machine EURO-KUW-2000 (Fischer KG Bielefeld, Germany). In case of wild potatoes or small tubers of interspecific crosses the starch content was calculated from dry matter. The methods are described by Haase (2003/04). Genes contributing to starch content are located on all chromosomes according a truly quantitative and polygenic determined trait (Yashina et al. 1973, Howard 1982, van Eck 2007). Considerable environmental influence is known (Dale & Mackay 1994). Combining of high starch content and late blight resistance is carried out in a special sub-programme at ZL; the results are described in 6.5.4.3. and 7.5.

4.6. Assessment of resistances, importance of the traits and its inheritance

4.6.1. Virus resistance

There are some 40 viruses infecting potatoes (Valkonen 2007). Breeding for virus resistance has a long tradition (Ross 1986); the current state is given by Zimnoch-Guzowska (2010). In our pre-breeding the frequency of occurrence of the following viruses in seed potatoes of each pre-breeding clone is tested yearly: PLRV (fig. 47), PVY, PVA, PVX, PVM and PVS. Because Gross Luesewitz is located in the "healthy region for seed potato production in M-WP" and at the same time within the „high grade region", which is officially recognized by EU (Wulfert et al. 2002), our seed potatoes in pre-breeding can be produced usually only *in vivo*, without *in vitro* culture. These conditions result in very low infection pressure from surrounding potato fields and require growing of only tested seed potatoes, early effective elimination of virus infected plants, protection against aphids and observance of given limits of virus infections in the breeding garden. Given regulations include testing of own clones and potato material received from outside for occurrence of harmful organisms before planting.

In chapter 5 is stressed that most sources of late blight resistance are highly susceptible to virus infections. This susceptibility has to counteract by breeding for virus resistance. Therefore information on resistance level to viruses of the pre-breeding material has to get from another location. Before 1991 Bernburg was used, then Aschersleben and since 2007 Quedlinburg as the main location of JKI. All three sites are located in a region with very early aphid fly and sta-

ble high population densities of aphids. From harvested A-clones at Gross Luesewitz 10 tubers each are stored for growing in a field assessment for virus resistance; these tubers are largely free of PLRV, PVY, PVA, PVX and PVM. Growing is conducted for three years successively without selection. Beside test clones infected plants are grown in border rows and each 20th row in-between. Insecticides are applied only against Colorado beetle. Symptoms of virus diseases are registered first decade of July of each season. One tuber per plant is harvested for seed for second and third season, respectively. Additionally one tuber per plant is taken at harvest from second year of growing for excised-bud assay (fig. 48) and ELISA (fig. 49); two tubers per plant are used of the third year for visual diagnosis of virus infections after growing in the greenhouse and for ELISA. Standard cultivars are grown with five replications, breeding clones with one.

4.6.2. Nematode resistance to *Globodera* species

Assessment of nematode resistance was carried out by Dr. Kruse in Office for Plant Protection Mecklenburg-West Pommerania at Rostock, now Department Plant Protection of Office for Agriculture, Food Security and Fishery. Plants were grown in 7 cm-pots in greenhouse, one plant for inoculation with about 2,000 grubs per 100 cm^3 soil of *G. rostochiensis* Ro1, two plants for Ro2, Ro3, Ro5 and *G. pallida* (Stone) Pa2 and Pa3 each. *G. pallida* was tested with population „Kalle" for Pa2 and „Delmsen" (since 2006 „Chavornay") for Pa3. Standard cultivars were Grata, Tanja, and Darwina. A clone was considered to be resistant to *Globodera rostochiensis* Ro1 with maximal one cyst per pot, however, to Ro2, Ro3 and Ro5, Pa2 and Pa3 up to seven cysts per pot (Dr. Kruse, personal communication 2000, 2006). Standards were Grata, Quarta and Ponto.

Resistance to *G. pallida* is mainly quantitatively inherited, whilst resistance against *G. rostochiensis* is assumed to be mainly monogenic or digenic inherited, partly with modifying minor genes (Phillips 1994). However, a major disease resistance locus (QTL) is ongoing to be characterized on chromosome IV acting against *G. pallida* Pa 2/3 (Griffin et al. 2011).

4.6.3. Resistance to *Erwinia* sp., *Fusarium* sp. and *Synchytrium endobioticum*

Assessment of tubers resistance to *Fusarium coeruleum* is conducted as described by Langerfeld (1979) after 1993. Earlier the tubers were injected with *Fusarium sulphureum* using a syringe (Hahn 1974). It is assumed to be a quantitative trait determined by polygenes as resistance to *Erwinia* sp. Burkhart et al. (2007) found a broad-sense heritability of 0.63-0.81, but only non-additive genetic variance in a diploid population.

Resistance to *Erwinia*-soft rot was assessed by F. Niepold (BBA Braunschweig) according to Langerfeld (personal communication) after 1993, before that time according to Hahn (1974) by injection of whole tubers. Few years' additional assessment in Aschersleben (JKI Quedlinburg) by R. Zielke was carried out in parallel. *Erwinia carotovora* ssp. *atroseptica* produces pectatlyases which degenerate pectin's of cell wall of potato tissue (Wegener 2002). 12 QTL are related to soft rot resistance located on 10 chromosomes (Zimnoch-Guzowska et al. 2000). Both, GCA and SCA play a significant role in the inheritance of resistance to soft rot. Several seasons of assessment are necessary due to environmental effects (Lebecka et al. 2004).

At Gross Luesewitz combined assessment of resistance of tubers against *Erwinia carotovora* ssp. *atroseptica* (10^4 cells/ml) and *Fusarium sulphureum* (10^4 conidia/ml) was carried out by dipping of a sample of 20 tubers per clone in four litre suspension after damaging it 30 seconds by falling in a drum-type sieve before inoculation (Weber et al. 1989). Improved quantitative soft rot resistance is expected to increase the threshold of soft rot outbreak by about hundredfold. This combined test method proved to enable more effective selection. Calculation with two standard cultivars over three years and four replications resulted in a lowest significant difference of 0.6 scores or 10% rotting tubers – much lesser than in pure test for *Erwinia*-soft rot.

Breeding for resistance to potato wart disease caused by *Synchytrium endobioticum* is success-

fully since more than 100 years due to use of race-specific hypersensitivity, its simple inheritance, and low distribution of soil-borne pathogen (Schick & Hopfe 1962). However, some of the resistance observed is likely to be conditioned, at least in part, by polygenes, which partly may operate as modifiers (Wastie 1994, Song et al. 2011). Resistance to potato wart as a subject of legislation has been tested on 10 tubers per pre-breeding clone in JKI at Kleinmachnow or Braunschweig since 1997 according to Langerfeld and Stachewicz (1994) and Stachewicz et al. (2005).

Limit values are in operation for incidence of tubers with scurf, *Fusarium*-dry rot, *Erwinia*-soft rot and tuber injuries in seed and table potatoes.

4.7. Estimation of traits during growing season on the field

Date of planting and date of emergence of 67% are registered. Uniformity of emergence (score 9-1) is recorded visually. The 15 plants of a plot emerge with a difference of up to three days for score 9, four days in case of score 8. Emergence varies about 5-6 days between first and last plant for score 7, 7-8 days for score 6, 9-10 days for 5, 11-13 days for 4, 14-17 days for 3, 18-22 days for 2, and still longer for score 1. These periods may be longer or shorter depending as well from whether conditions in April and May as from storage conditions and pre-sprouting. Long-term data of standards helps to adapt the scale.

Juvenile haulm growing (9-1) describes speediness of growth during first about three weeks after emergence, which influences assimilation rate, yield mainly of early clones, and weed cover. Score 9 means very speedy, score 5 medium, and score 1 extremely slowly growing as in case of some wild species. The final number of plants per plot is registered. Haulm mass (9-1) is estimated 8-10 days after flowering with score 9 for its maximum and 1 for nearly no haulm. Reach haulm development causes best soil cover and weed cover, however haulm mass 8 and 9 exceeds optimum for high yield and support blight infections by its microclimate. Standards were scored with following long-term results: Karlena 6, Marabel 4.5, Agria 5, and Jelly 6. Flower colour is directly put down; scale 1-9 is too short to consider all differences. The range of intensity of flowering is scored 9 (very reach) to 1 (not flowering) from experience, orientating by standard cultivars. As for most traits clone-specific development requires several times observations at appropriate intervals during growing season and partly correction of formerly given data. Facility visually to diagnose virus infections (9-1) requires sufficient experience in seed potato production to minimize virus diseases by early selection of infected plants. Because more than six virus diseases with different symptoms are to consider, which are clone-specifically expressed, morphological factors as leave structure and its colour are important, since they affect the possibility to diagnose visually virus diseases. This trait defies simple explanation. Score 9 stands for easily to indicate, score 1 for not perceptible. Differentiation is most difficult for scores 4-6, at which score 4 is still to tolerate for dihaploids, not for tetraploid material. The part (%) of plants with stunting and rosetting of plant tops by *Rhizoctonia solani* and of blackleg caused mainly by *Erwinia carotovora* ssp. *atroseptica* is recorded during whole growing season. Plant height (9-1) is stated visually at the end of flowering: >110 cm coincides with very high and score 9, score 2 corresponds with 10-15 cm high, score 1 with about 5 cm. Low GCA, SCA and maternal effect of genetic variance are mentioned (Bradshaw & Mackay 1994).

Stability of haulm in field (9-1) varies from very stable (9) over middle (5) to only lying stems, score 1. Repeated estimation is necessary in period of full developed haulm mass up to the beginning of maturation after a day with violent wind. Maturation reduces the stability; therefore scoring at the same physiological stage of clones is important. This trait potentially affects infections of haulm, favoured by humid conditions as late blight. Clones scored below four are rejected. Leave type (score 1) und stem type (score 5) describe the range of growing habit. Intermediate stage of leave/stem-type (score 3) occurs most often. Standard cultivar Karlena got

in average score 2.5-3, Marabel 2.5, Agria 2.5, Kuras 3, and Sarpo Mira 4. GCA and SCA take part on genetic variance of the haulm type with midparent-progeny correlation r = 0.55 (Bradshaw & Mackay 1994).

Maturity is in pre-breeding for late blight resistance a very important trait depending upon a high number of genes and being mainly heterozygous for most of these (Schick & Hopfe 1962, Howard, 1982). Three QTL for foliage maturity are identified on chromosome IV, V, and VI by Ruofang et al. (2005). Differences in number and size of stomata and regulation of its function were found at Gross Luesewitz as being connected with maturity (Meinl & Moeller 1961). Already Schmidt (1933) mentioned that evaluation of maturity is not easy. The method of estimation in breeding is under discussion in many institutes. For instance in INRA plant high is used as indicator of maturity (Ellissèche et al. 2005). In pre-breeding at Gross Luesewitz all B- to D-clones of 2006 were assessed with three methods in parallel: 1. scoring of course of haulm yellowing, 2. number of days from planting to dying of haulm, 3. number of days from emergence to dying. Estimation according to course of haulm yellowing requires as the other several dates for rating of the breeding material per season. Two suitable dates are fixed for each of the three groups very early to early, second early, and second late to late in an interval of 5-10 days by means of well known standards. So a good differentiation over the whole range is possible. Standards are the following with its long-term maturity score: Solist 8.5, Marabel 7.5, Karlena 6.8-7.0, Likaria 5-5.5, Agria 4.0-4.4, Jelly 3.0-3.2, Kuras 2.6-2.7.

Another possibility of characterization of maturity considers the number of days from planting to dying of 97% of haulm. Approximate values are the following: very early up to 110 days, early 110-129 days, second early 125-145 days, second late 140-170 days, late 165-185 days, very late more than 185 days. A variation between 70 and 200 days assume Schick and Hopfe (1962). This method seems to be more simple and objectively. However, variation from year to year is higher than it is based yellowing. Moreover, all other causes of dying are included as mistakes.

A third method to assess maturity counts the number of days from emergence to dying of 97% of haulm (days of growing season). This variant takes highest sacrifice of time. In 2006 Marabel took 76 days, Karlena 82, Adretta 91, Agria 87, Steffi 101, Jelly 109, Kuras 131. Both „objective" methods required more working time and correlated with each other, r = 0.51 (tetraploid material) respectively r = 0.96 (dihaploid). With scoring according to yellowing they correlated r = -0.43, -0.68 on tetraploid material, r = -0.75; -0.76 in case of dihaploids. An experienced person can exclude above mentioned mistakes in scoring yellowing, because in that stage other causes of premature dying are visible.

GCA is stated to be the main component of genetic variance of maturity; maternal effects occurred. Midparent-progeny correlation is given with r = 0.72 (Bradshaw & Mackay 1994).

At the end of a dry and hot period level of wilt on early afternoon was estimated as indication of drought tolerance. Suitable climatic conditions for this trait occurred very rarely in the field during decades at Gross Luesewitz, but happened in 2006. At Aschersleben the growing period 2004 was characterized by long time dryness. Wilt and poor development are scored 1-9, but a simple scale can not be described. Reach experience concerning healthy and normal plant reaction enables adaptation of the scale, excludes biotic and other abiotic reasons and considers ploidy level of the material. A method suitable for assessment in breeding practice seems not available (Iwama et al. 2005, Balko 2008). However, studies go on to several QTLs and candidate genes (Anithakumari et al. 2010).

Incidence with *Alternaria* sp. (early blight) and *Botrytis* sp. (grey mould) is as usually separate registered, but because of very often occurrence at the same time in 2006 it is scored together (fig. 50-53). Intensity of incidence was scored according to the scale used for foliage blight (table 16). High susceptibility of *S. demissum* to *Alternaria* sp. was mentioned by Wriedt (1955). As well *Alternaria solani* as *Alternaria alternata* were detected in potatoes (Hausladen 2006). Five

QTL are identified for early blight resistance in a dihaploid population on chromosome IV, V, IX, XI, and XII (Ruofang et al. 2005), which hints to a polygenic trait. Turkensteen and Spoelder (2011) found that in the Netherlands Alternaria-like lesions often were not caused by *Alternaria solani*, but boron deficiency could has been increased susceptibility to damage by ozone in 2009 and 2010.

4.8. Assessment of additional traits on tubers and its inheritance

Stolon length of wild species can reach two meters; it is one of the first noticeable undesired, "wild expressions" of traits (fig. 54). Intensive stolon development which leads to new shoots instead of tubers indicates unsuitable photoperiodic growth conditions (Kopetz & Steineck 1954). Stolon length varied within an accession of wild species too, for instance *S. demissum*; it is genetically determined and is considered in pre-breeding from seedlings stage on by visual scoring and early selection. Score 1 means extremely long stolon, score 9 very short one. It should be mentioned that on variety level differences in stolon length at four-leave-stage of seedlings are correlated to maturity (Engel & Moeller 1959).

Yield is known as a classical quantitative and polygenic determined trait on which other traits are involved as for instance, intensity of assimilation and dissimilation, maturity, ability to take up nutrients and water as efficiency of its utilization. Dominant and recessive genes seem to be responsible, heterosis is mentioned, environmental effects in a wide range are described (Schick & Hopfe 1962, Yashina et al. 1973). The genetic components of variance GCA and SCA, both are important; midparent-progeny correlation r=0.14-0.55 is given by Bradshaw and Mackay (1994). Because of extremely low yield of wild clones as sources of late blight resistance in the field in long day conditions, pre-breeding has to go a long way to improve this trait step by step to nearly the cultivar level. A side effect of broadening the genetic basis of *S. tuberosum* ssp. *tuberosum* in this pre-breeding, for instance by genes from *S. demissum*, could be heterosis on yield, as it is described by Toxopeus (1952). In pre-breeding tuber yield (g/plant) is weighed during four successive years from one location and nine plants per plot of the first year (A-clone) and 15 plants per plot of the following years (B- to D-clone). The number of tubers per plant is counted (per plot) and calculated per plant. Howard (1982) recommended never crossing two clones, which both have numerous tubers because of its heritability, which results in a higher part of too small tubers. GCA seems to be more important than SCA with midparent-progeny correlation of r = 0.57-0.71 (Bradshaw & Mackay 1994). The mean tuber weight is calculated. On its expression the genetic components GCA, SCA and maternal effect are involved; a midparent-progeny correlation of r = 0.4-0.81 is stated (Bradshaw & Mackay 1994).

General impression of tubers includes all external tuber traits including size, variation of size and effect of diseases. Score nine means ideal, score one expresses the negative extreme. The estimation has to be learned, it can not simple be described. Good impression corresponds to score seven (fig. 55), for table and processing purpose score six should be obtained at least. Score five is sufficiently for starch potatoes. Progeny of BC1 and BC2 often get score three or four, species crosses often lesser. Uniformity of tuber size of a clone considers variability of tuber size and the saleable part. Size distribution of potato tubers are defined by the degree of stolon branching, the duration of stolon tip swelling period, tuber growth rate and tuber resorption. All these parts interact and are under environmental influence, its inheritance is very complex (van Eck 2007). In breeding of cultivars and its assessment size grading is carried out by a grading machine, the weight ratio of different fractions is recorded. For pre-breeding quickly visual estimation does instead of weighing of fractions. Score nine is given for very uniform saleable tubers, score five means a middle range with about 15% unsaleable tubers. Scores 1-3 are used mainly in case of wild material or BC1.

Visual scoring of tuber size with 9-1 describes very large to tiny. The graduation of material

grown in greenhouse differs from that grown in the field. Known standard cultivars help to adapt the scale. Tuber size and tuber number are negative correlated and relate to number of stems.

Following encoding (9-1) of skin colour is used: white (9), bright ochre (8), ochre (7), grey brown (6, fig. 56), bright red (5), red (4), dark red (3), bright blue (2), and violet (1). Red or blue eyes, pigmentation in a zone around the eyes, pigmented eyebrows, blue or red blots on ochre skin, or lack of pigmentation around the eyes of a coloured tuber are additional recorded. Differences between uncoloured skin (score 9 to 7) are influenced by underlying tuber flesh colour. Red and blue are dominant over uncoloured; red skin colour is changed to blue by an additional dominant gene (Schick & Hopfe 1962). Mainly simple inheritance is known (Ortiz & Huaman 1994, van Eck 2007). Appearance and touching of tuber skin enable scoring of roughness of skin (1-9). Very cracked skin is scored one, cracked skin get two, score three means scaly skin, four very rough (see Fig. 56), five netted (fig. 57). Score six is given for rough skin (fig. 58), seven for a bit rough, eight for smooth (fig. 59) and nine for very smooth (fig. 60). European breeders prefer a thin, smooth, shiny and transparent skin for washed and pre-packed potatoes and for serving unpeeled potato dishes. The inheritance of most skin-related characters is largely unknown (van Eck 2007). Up to 1992 insensitiveness to mechanical damage was an additional breeding objective in our pre-breeding, which supported rough to very rough skin. Since the late 1990ies attention was paid to smooth skin.

Negative aspects of tuber shape are integrated in trait shape defects (9-1) as angular, flat, pear-shaped (fig. 61). Score nine shows ideal shape longitudinally and crossways without defects on hilum (7-9) and eyes (7-9). About 5-10% of tubers may be a bit pear-shaped or a little flat or angularly in case of score eight. For score seven up to 15% may be a bit pear-shaped and up to 20% a bit angularly. Next step (score 6) corresponds to 20% moderate pear-shaped and 30% a bit angularly. Score five may include 30% pear-shaped, 30% moderate angularly or 50% a bit angularly. A sample with 40% pear-shaped tubers and 40% middle strong angularly or 70% moderate angular tubers gets score four. 67% or 85% strong pear-shaped and strong angular tubers are scored three or two, respectively. Extremely deformed tubers get score one.

The form of hilum (1-9) influences tuber injury and infections during harvest and handling operations. Score nine means the hilum is not easy visible. If hilum is partly inconspicuously score eight is given. Score seven corresponds with good identifiable hilum without hollow around it. If 30% of tubers have a bit prominent hilum or little hilum hollow, score six is given. Small prominent hilum or little hilum hollow at 50% of tubers or its combination 40%/30% result in score five. Prominent hilum (fig. 62) at 70% of tubers or 50% with moderate hilum hollow or 50% prominent hilum and 30% moderate hollow characterises score 4. Score three corresponds with about 100 % prominent hilum or 60% moderate hilum hollow or 70%/40% of both. Score two means 100% long prominent hilum or 85% deep hilum hollow or its combination at about 70%. The negative extreme gets score one.

Tuber shape in longitudinal direction (1-9) has the following scale: kidney-shaped (9), very long (8), long (7, fig. 63), long-oval (6, fig. 64)), oval (5, fig. 65), round-oval (4), round (3), cross-oval (2), elliptical (1). Long shape was assumed to be dominant to round including at least four genes with cumulative effects (Howard 1970), whilst Schick & Hopfe (1962) assumed polygenic determination with partly intermediately effecting genes and modifiers. Recently, the single-gene hypothesis is maintained with multiple alleles at the Ro-locus (van Eck 2007). GCA and SCA take part on genetic variance with midparent-progeny correlation of $r = 0.5$ (Bradshaw & Mackay 1994).

Tuber shape crossways is estimated looking in direction of tuber longitudinal axis. Ideal is a full round form (score 9, which is nearly reached in fig. 66). Steps from round (9) to even (flat, 1) are graphically represented and directly used as help. The relation of larger to the smaller diameter changes from score eight to score three nearly as follows: 1:0.9, 1:0.8, 1:0.7, 1:0.6, 1:0.45, and

1:0.3. Score two means flat lens-shaped. Score one means extremely flat and was very rarely found in wild material. Resistance to tuber skinning injury (1-9) is important to reduce losses and contain tuber quality. Tuber wounds cause water vapour loss, which increases shrinkage, promotes flaccidity, and exacerbates black spot, bruising and sprouting - all these have to be avoided. Other results of wounding are increased respiration and danger of infection by wound pathogens leading to tuber rots. The natural surface colour of excoriated areas is not re-established after wound healing. Tuber cells exposed by injuries must wound-heal to generate waxes, a suberized closing layer and the associated suberized wound periderm. Suberin biosynthesis and accumulation on cell walls is a major part of wound-healing; its pathways, mechanisms, and genes involved are unknown or tentatively (Lulai 2007). Score nine means very stable skin-set. In case of score five excoriation requires medium tangential force, score three is given for samples mainly excoriated by usual harvester. Nearly total loss of skin corresponds to score one. Good agricultural practice makes this trait subordinated. If late maturing clones are ranged by mistake in an earlier growing trail, then too early harvest leads to problems. Susceptible clones are discarded.

Number of lenticels per tuber (1-9) and size of lenticels (1-9) were assessed for special research, not in general in pre-breeding. If no lenticels were visible, score nine was given. Score one corresponded with the maximal number found on 4 cm^2 in average of three times count per tuber, five tubers per clone. The lenticel's size was estimated from very little (9) to very large (1). Lenticel size two is shown in figure 61. Figure 67 has frequently (score 3) very large lenticels (1) on ochre, a bit rough skin.

Eye depth (1-9) influences the proportion of wastage due to peeling. Already seedlings are selected for it, which varies from extremely deep (1) over deep (3, as in some old cultivars) to middle (5). Score seven means shallow eyes; score nine means very shallow eyes, which are difficult to identify. There are results showing deep eyes are inherited dominant to shallow ones and others reverse, interpretations of known studies have a wide range up to polygenic inheritance (Schick & Hopfe 1962, Howard 1982, Ortiz & Huaman, 1994). Inheritance of eye depth is not understood (van Eck 2007). GCA was the main genetic component with a midparent-progeny correlation of r = 0.78 (Bradshaw & Mackay 1994).

Dormancy is assessed on samples of 5-10 tubers stored cold, dry and dark up to beginning of January and then at about 15°C so long that standard varieties reached a typical stage of sprouting and only few clones did not beginning to sprout. Very long lasting dormancy is scored nine, whilst very short dormancy get score two. Missing of dormancy (score 1) is visible at or after harvest and such clones are immediately eliminated. The differentiation from score 9-2 is assessed in March (fig. 68). Long dormancy contributes to keeping quality as an important trait, but it is correlated with slow juvenile haulm growth. Contradictionary results are described concerning the inheritance of dormancy (van Eck 2007). Several loci are involved in dormancy control (Vreugdenhil 2007). Ewing et al. (2004) identified eight QTL for tuber dormancy on chromosome II, III, V, VIII, IX, X, and XI.

The percentage of tubers is estimated with external and internal defects as cracked, hollow heart, internal rust spot (fig. 69), and second growth from the crop of 15 plants about three weeks after harvest. No single physiological/biochemical parameter has been identified which underpins these disorders (Davies 1998). Negative selection against these defects is common in cultivar breeding and in pre-breeding; GCA and SCA play a role in inheritance of these traits (Bradshaw & Mackay 1994). Incidence of tuber scab (fig. 70), black scurf (*Rhizoctonia solani)* and deformed tubers is scored according to table 22. Besides the percentage of invaded tubers intensity on single tubers is considered.

Table 22 Scale for scoring of tuber scab, black scurf and tuber deformation

Score	9	8	7	6	5	4	3	2	1
Incidence (% of tubers)	0	0.5	3	6	15	33	67	83	97

Occurrence of tuber scab is highly influenced by environmental conditions. On table potatoes scab handicaps its selling and excludes its offer as washed potatoes. Resistance to scab seems to be caused morphologically and physiologically by several genes (Schick & Hopfe 1962). Research of genetics of scab resistance shows results difficult to interpret. Results are published for monogenic determined resistance, for cytoplasmatic influences and polygenes with high GCA component for *Streptomyces scabies* (Wastie 1994). New causal agents of scab (other species than *Streptomyces scabies*) are detected (Bouchek-Mechiche et al. 1998, Valkonen 1998, Valkonen et al. 2002) and complicate resistance breeding to scab (Pasco 1998). Infections of the sprouts or stems with *Rhizoctonia solani* cause uneven and irregular emergence, branched stems, stunting and rosetting of plant tops, formation of aerial tubers; infected tubers may be deformed, show scab-like patches or are not sprouting. Infection often starts from dark sclerotia on surface of seed tubers (Turkensteen 1996). Hitherto research to find significant differences in resistance to this complex failed to show chances for breeding against this highly environmental influenced disease.

5. Use of wild and cultivated potato species as sources of quantitative late blight resistance

5.1. Late blight resistance in wild and cultivated species of potato

5.1.1. Expeditions, gene banks and systematics of potato

89 host species of *Phytophthora infestans* are listed by Erwin and Ribeiro (1996). The potato possesses more related wild species than any other crop plant: 128 living and 191 accepted species according to the systematics of Hawkes (1990). Other taxonomic systems originate from Correll (1962), Bukasov (1973), or Ochoa (1990, 1999). Seven cultivated and 121 wild species are differently distributed in its native habitats between other plants from south-west USA and southern Chile with a wide range of ecological diversity since more than 10,000 years. Since Vavilov (1935) postulated 'centres of origin of cultivated plants' in 1926 more than 80 taxonomists and potato researchers have collected tuber-bearing potato samples from its native locations, starting with expeditions of Bukasov in 1925, Juzepczuk in 1929, Baur and Schick in 1930/31 and continued up to last years (Hawkes 1979a, Schueler 1999, Huaman et al. 2000). The intention was to make available new sources for potato breeding. Discovery of new wild potato species is not finished (Huaman & Schmiediche 1999). Peru has the highest number of species with an extraordinary part of rare species. High species richness occurs in Northern Argentina, central Bolivia, central Ecuador and central Mexico (Hijmans & Spooner 2001). It's retaining by cultivation, propagation and storage in gene banks enabled description, evaluation and use in breeding. Cytogenetic, biosystematic and pathologic research goes on. Parental line breeders incorporate genes for desired traits from wild species into cultivated potato before variety breeding can utilize such pre-breeding material for enhancement of new varieties.

Two centres of diversity of potato species can be recognized (Hawkes 1990), one in central Mexico and the second in the high Andes (Peru, Bolivia, north-west Argentina). At the same time the highest genetic diversity of host reaction to *P. infestans* (Niederhauser 1991, Budin 2002) and the highest pathogenic variability of isolates of *P. infestans* to potato and other hosts (Galindo

& Gallegly 1960, Goodwin et al. 1992) were found in central Mexico. According to Vavilov (1935) here the longest co-evolution with the pathogen has been happened on the centre of origin of *P. infestans* (Niederhauser 1991, Goodwin 1996) and a secondary centre of origin of potato species (Correll 1962), both types of resistance to late blight developed in different frequencies and varied quantitative levels.

Worldwide about 15,000 wild potato accessions are being maintained in large collections from which about 50 % are unique (Hoekstra (2009). The gene banks are integrated in Intergene bank Potato Database (IPD) which contains 7112 accessions of 188 taxa of tuber-bearing wild potatoes (Huaman et al. 2000). Potato samples from expeditions are named accessions which are maintained and propagated by seeds or tubers or are cultivated *in vitro*. Their species name is to decide; abbreviations of the species names are used according to Huaman and Ross (1985). The value of an accession depends from freedom of diseases and expressed traits. Systematic evaluation of the accessions in gene banks for diverse traits is globally not finished. Single plants of an accession usually vary, sometimes in a wide range. If single plants with a determined quantitative level of resistance occur within an accession it is listed as possessing resistance. However, one has to consider that different authors used different methods, tested from different growing conditions in different physiological stages of the plants and estimated resistance different stringently. So the outcome is different reliable-looking for breeders, a differentiation according to the resistance type is difficult, particularly in Mexican species and often to consider as preliminary. Nevertheless, gene bank data give a hint, in which accessions of which species a suitable level of quantitative resistance can be expected in a part of individuals, which are to select after own assessment from a seed sample. Data are available for more than 33,000 evaluations of wild potato accessions covering 55 traits (Bradshaw et al. 2006c).

Whilst in past wild material was tested for resistance by inoculation with the oomycete, in EU project BIOEXPLOIT tagging of R-genes and resistance gene analogues (RGAs) was carried out by testing nearly 50 taxa with specific primers (Hoekstra 2009). Selections in gene banks for qualitative resistance (R-genes) occur intensively on molecular basis and consider preferred R-genes of cultivated species (Verweij et al. 2010).

5.1.2. Foliage blight resistance in species and native regions

Huaman et al. (2000) inform that among 2,738 accessions tested of the Inter-Gene bank Potato Database 1,024 (37%) have useful genes for foliage blight resistance. In CIP collection 19% of accessions with foliage blight resistance were found (Huaman & Schmiediche 1999). According to Hawkes (1990) resistance to late blight occurs in reliable level in *S. berthaultii, S. bulbocastanum, S. circaeifolium, S. demissum, S. microdontum, S. phureja, S. pinnatisectum, S. polyadenium, S. stoloniferum, S. tarijense, S. tbr.* ssp. *andigena, S. vernei, S. verrucosum*. Species with hypersensitivity usually additionally possess quantitative resistance to *P. infestans*. However the occurrence of quantitative resistance is wider than that of hypersensitivity. In the literature more than 60 species are mentioned to be promising as potential sources of foliage blight resistance (Lehmann 1938a, Mueller 1949, Rudorf et al. 1950, Rudorf & Schaper 1951, Niederhauser & Mills 1953, Black & Gallegly 1957, Niederhauser 1962, Toxopeus 1964, Ross & Rowe 1965, Kameraz 1968, Jeschke & Rothacker 1968, Budin 1970, Graham 1963, Thurston 1971, Zhitlova 1976, Chadayeva 1977, Lipski et al. 1978, Laptyev & Dzagoyeva 1979, Tikhenko 1979, Khramzova & Aleksandrova 1980, Ochoa 1981, van Soest & Seidewitz 1981, Huaman 1982, van Soest & Hondelmann 1983, Plaisted 1983, van Soest et al. 1984, Brown & Stewart 1988, Zoteyeva 1984a, 1988, Colon et al. 1987, Foldø 1987, Schmiediche 1987, Osiecka 1988, Rivera-Pena & Molina-Galan 1989, Rivera-Pena 1990b, 1992, Darsow & Hinze 1991a, b, 1992, Rousselle et al. 1992, Colon et al. 1995b, Micheletto et al. 2000, Douches et al. 2001, Budin 2002, Kiru 2003, Zoteyeva 2003, Zlesak & Thill 2004, Simko et al. 2007, Hoekstra 2009, Jakuczun et al. 2010, Trognitz et al. 2010). Besides the above mentioned species the following are found to be partly resistant: *S. acaule*, *S. andreanum*,

S. boliviense, *S. brachistotrichum*, *S. brachycarpum*, *S. brevicaule*, *S. candelmanium*, *S. capsicibaccatum*, *S. cardiophyllum*, *S. chacoense*, *S. chiquidenum*, *S. chomatophilum*, *S. columbianum*, *S. x curtilobum*, *S. ehrenbergii*, *S. fendleri*, *S. gourlayi*, *S. guerreroense*, *S. hougasii*, *S. hjertingii*, *S. jamesii*, *S. iopetalum*, *S. lanciforme*, *S. macmillanii syn. S. stenotomum*, *S. marinasense*, *S. morelliformae*, *S. multidissectum*, *S. multiinterruptum*, *S. oplocense*, *S. oxycarpum*, *S. papita*, *S. polytrichon*, *S. quimense*, *S. rybinii*, *S. salamanii*, *S. x sambucinum*, *S. x semidemissum*, *S. simplicifolium*, *S. sparsipilum*, *S. spegazzinii*, *S. stenotomum*, *S. sucrense*, *S. toralapanum*, *S. trifidum*, *S. x vallis-mexici*, *S. venturii*, *S. vitaurrei*, *S. yungasense.* Additionally foliage blight resistance is found in *S. alandiae*, *S. albicans*, *S. ambosinum*, *S. cajamarquense*, *S. coelestipetalum*, *S. commersonii*, *S. huancabambense*, *S. irosinum*, *S. megistacrolobum*, *S. piurae*, *S. sogarandinum* (Perez et al. 2000). Zoteyeva (2005) mentioned additionally quantitative resistance in *S. neoantipoviczii* syn. *S. stoloniferum* and *S. ruiz-ceballosii* syn. *S. sparsipilum*. Only the half of 20 species listed by Simko et al. (2007) for foliage blight resistance is confirmed by our results to have a sufficient high level of quantitative blight resistance to be used in breeding. Most of these assessments are conducted under long-day conditions and therefore are to see with reservation as to be overestimated due to its extreme lateness (be assessed in a to early stage of growing).

According to Toxopeus (1956b) desired genes are not so much restricted to certain species as to certain areas. Clones of the same species from drier zones are often susceptible and from nearby higher rainfall areas are uniformly resistant (Niederhauser 1991). Budin (2002) defined four "genetic centres of formation of potato species possessing resistance to late blight" from data of literature and results of VIR St. Petersburg:

1. southern Mexico between 18-21°N, 98-102°W, at altitudes from 1900 to 3100 m, in the states Mexico, Destricto Federal, Michoacan, Morelos, Pueblo, Hidalgo, Veracruz, Oaxaca, Guanajuato, and Jalisco;

2. Columbian-Ecuadorian centre between the rivers Cauca and Magdalena, between central and eastern Cordilleras, in the departments of Narino and Cauca in Columbia, and in the Imbabura department in Ecuador, in all about 250 km long;

3. Bolivian centre embraces the departments Cochabamba and Chuquisaca on the eastern slope of the Andes, 17-19°S and 65-77°W;

4. Argentinean centre includes the Tilcara valley, the foothills of the North-east, and provinces Salta and Juhuy between 22-25°S and 64-65°W in altitudes from 1500 to 3000 m.

Below an altitude of 1200 m and above 3000 m donors for blight resistance were not detected (Budin 2002). Ochoa (1954) assumed development of resistance in a part of North Peru. Probably focussing on the accessions from places of discovery within the mentioned regions could increase the efficiency of selection of potentially donors of resistance. However, two points of view are additionally to consider:

1. Foliage blight resistance for long-day conditions has to be assessed with separation of the maturity effect (see chapter 2.5, 2.7, 4.2.4); the sources of resistance are short-day adapted.

2. Resistance to tuber blight is more independently expressed from resistance to foliage blight and may have lesser importance outside of temperate climate (Andrivon 1994, Garzon & Forbes 1999).

However, if resistance on foliage and tubers is intended in breeding its combination in the source of resistance is to prefer rather than combination in later breeding stage. Generally the tendency exists to overestimate the foliage blight resistance of short day-adapted wild material in long day conditions because of it's physiologically too early stage of testing even in the end of September when tuber initiation begins (Darsow et al. 1988). The photoperiodic adaptation depends on the latitude and is more stringent the higher the altitude of the place of origin of an accession (Junges 1970).

Species with foliage blight resistance, but with too susceptible tubers are according to our results in GLKS: *S. andreanum, S. berthaultii, S. boliviense, S. capsicibaccatum, S. chiquidenum*, *S. columbianum, S. curtilobum, S. guerreroense, S. huancabambense, S. iopetalum, S. marinasense, S. microdontum, S. multidissectum, S. oplocense, S. phureja, S. piurae*, *S. polyadenium, S. semidemissum, S. sparsipilum, S. spegazzinii, S. sucrense, S. stenotomum, S. tarijense, S. vallis-mexici, S. venturii, S. vernei, S. verrucosum, S. yungasense* (Darsow 2000b). Its use requires later addition of tuber blight resistance with the consequence of one additional cross step, if a suitable inheritor is available.

5.1.3. Tuber blight resistance in species

In the literature information about tuber blight resistance of wild species is rarely because of tuber size is frequently only few mm (fig. 72-75). Therefore mainly cultivated species are tested. In CIP collection 24% of accessions with useful genes for tuber blight resistance were found (Huaman & Schmiediche 1999). Quite unexpected is that tuber blight resistance was stated in 1,041 accessions among 1,193 tested ones (Huaman et al. 2000), since tuber blight is to find very lesser frequently than foliage blight (Antonov 1974, Glendinning 1989, Darsow et al. 1993). This fact tells a lot about reliability of applied assessment methods. Tuber blight resistance is detected in *S. tuberosum* ssp. *andigena* (Antonov 1974, Khramcova & Aleksandrova 1980, Huaman 1987), *S. phureja* and *S. rybinii* (Zoteyeva 1984b), *S. stenotomum* (Huaman 1987), *S. bulbocastanum, S. cardiophyllum, S. demissum, S. ehrenbergii, S. jamesii, S. microdontum, S. pinnatisectum, S. polytrichon, S. vernei* (Chadayeva 1977), *S. stoloniferum* (Kotova 1981), *S. cardiophyllum* and *S. spegazzinii* (Zoteyeva 2006). Tuber blight resistance is additionally found by Zoteyeva (2005) with test in laboratory in *S. albicans*, *S. antipoviczii* syn. *S. stoloniferum*, *S. berthaultii*, *S. brevicaule*, *S. chacoense*, *S. famatinae* syn. *S. spegazzinii*, *S. fendleri*, *S. hougasii*, *S. kurtzianum*, *S. parodii*, *S. papita*, *S. simplicifolium*, *S. sparsipilum*, *S. spegazzinii*, *S. sucrense*, *S. subtilis.* According to field observations moreover 20 species are mentioned with tuber blight resistant individuals; such results are only delimited reliable because of unknown isolates and foliage-attack depending infection pressure. Toxopeus (1956b) tested several traits not before F1 or BC1 from cross with *tbr*. Assessment of tuber blight resistance at IK/ILK Gross Luesewitz involved all tuber-bearing species in GLKS grown in greenhouse. The photoperiod determines the development of tubers, but timing of dry periods has been influenced whether during co-evolution resistance of tubers has had a survival advantage. This was not necessary for instance, where winter dry climate exists in parts of Peru in opposite to summer dryness in parts of Chile (Junges 1957, 1962). Tuber development in regions of Peru (Toxopeus 1955) and from *S. vernei* in Argentina (Bruecher 1990) occurs in a period without rain. So in accessions of species of these regions a determined level of foliage blight resistance is found without tuber blight resistance. Such material should be used as source of blight resistance only if it is connected with important advantages from other traits. Among the species of GLKS tested at Gross Luesewitz were 95 with low frequency or without a usable level of quantitative tuber blight resistance. Eight species had good resistance in a low part of its accessions (average of accession); seven in 20-45% of accessions and 13 species were characterized by frequently high tuber resistance (Darsow & Hinze 1991b). Species with high level of tuber blight resistance after long-term assessment (1967-2007) are listed in the following table 23.

Table 23 *Solanum*-species of the Gene Bank Gross Luesewitz (GLKS) with accessions highly resistant to tuber blight resistance in scale 1-9, state 2007, authorship: U. Darsow, H. Oertel, T. Hammann, E. Hinze, K. Schueler, K. Dehmer, M. Vandrey, systematics of Hawkes (1990).

		Number of accessions with score average of tested individuals		
Species	Series	score 9	score 8	score 7
S. acaule	ACA	0	1	7
S. ambosinum	TUB-W	0	0	1
S. bulbocastanum	BUL	4	20	4
S. arrac-papa	TUB-W	0	0	1
S. brachycarpum	DEM	0	0	2
S. brachistotrichum	PIN	0	0	1
S. brevicaule	TUB-W	0	0	1
S. cardiophyllum	PIN	0	5	8
S. chacoense	YNG	0	0	1
S. chancayense	TUB-W	0	0	1
S. chomatophilum	CON	0	1	0
S. colombianum	CON	0	0	1
S. demissum	DEM	4	40	80
S. fendleri	LON	0	2	1
S. hjertingii	LON	0	1	4
S. hondelmannii	TUB-W	0	0	1
S. hougasii	DEM	0	1	1
S. jamesii	PIN	0	1	0
S. lignicaule	LIG	0	0	1
S. leptophyes	TUB-W	0	0	1
S. megistacrolobum	MEG	0	0	2
S. mochiquense	TUB-W	0	0	1
S. morelliforme	MOP	0	1	0
S. multiinterruptum	TUB-W	0	0	1
S. neocardenasii	TUB-W	0	0	1
S. oxycarpum	CON	0	0	1
S. papita	LON	0	1	1
S. pinnatisectum	PIN	0	8	9
S. polytrichon	LON	0	3	2
S. x sambucinum	PIN	0	0	1
S. schenckii	DEM	0	1	3
S. stoloniferum	LON	0	9	26
S. tarnii	PIN	0	0	1
S. trifidum	PIN	0	0	4
S. tbr. ssp. *andigena*	TUB-K	0	2	3
S. violaceimarmoratum	CON	0	0	1

Accessions with tuber resistance average score six were additionally found in *S. agrimifolium, S. boliviense, S. columbianum, S. commersonii, S. ehrenbergii, S. goniocalyx, S. guerreroense, S. infundibuliformae, S. iopetalum, S. macmillanii syn. S. stenotomum, S. x michoacanum, S. punae, S. sanctae-rosae, S. schreiteri syn. S. acaule, S. sparsipilum, S. x sucrense, S. tuquerrense, S. whigtianum* of GLKS. Table 23 shows that high tuber blight resistance is mainly expressed in Mexican species. Of course, single tuber-resistant plants can be detected in more accessions and other species too but lower frequently and on a lower level. Sometimes unexpected resistance is explained by confounding or unintentional cross-pollination.

5.1.4. Evaluation of potato collection GLKS Gross Luesewitz for quantitative resistance of foliage and tubers to late blight

The gene bank GLKS was founded as part of the Institute for Plant Breeding at Gross Luesewitz in 1948. In 1972 it was renamed to the Institute of Potato Research Gross Luesewitz, since 1992 the gene bank belonged to IPK Gatersleben (Rothacker et al. 1991). The collection includes 133 wild and seven cultivated *Solanum*-species with 3,388 accessions besides 2,736 potato cultivars (Schueler et al. 2000, Dehmer 2011). GLKS is integrated in Inter-gene bank Potato Database IPD.

Blight resistance of *Solanum*-species has been assessed continuously by the group, responsible for pre-breeding of potato for resistance to *P. infestans* (Mont.) de Bary in the same institute, since 1992 in Federal Centre for Breeding Research on Cultivated Plants (BAZ), which is renamed to Julius–Kuehn-Institute in 2008, with methods described in chapter 4.2.2. and 4.2.3. for foliage blight resistance, 4.4.1. for tuber blight resistance. Resistance is expressed in a 1-9-scale of increasing resistance. Seeds of each accession are sown in an interval of 10-15 years to produce new seeds from a mini-population for storage, maintaining and demand of users in future. After harvest three tubers of each seedling were used to assess tuber blight resistance. 100 genotypes are intended to test for good characterization of quantitative level of resistance of an accession. Normally single tested clones are not maintained, if the accession developed true seeds. Each user has to select plants of interest from seed sample got from the gene bank.

Assessment of quantitative blight resistance of *Solanum*-species was started in 1960ies on detached leaflets (Jeschke & Rothacker 1968). Quantitative foliage blight resistance with score ≥8 in average of accession was found in only 14 species (Table 23). Highest probability to find clones with combined high resistance on foliage and tubers exists in *S. bulbocastanum*, *S. cardiophyllum*, *S. circaeifolium*, *S. pinnatisectum*, *S. trifidum*, *S. demissum* (fig. 71), *S. hougasii*, *S. polytrichon* and *S. stoloniferum*, in some extent already in *S. colombianum* and in *S. chomatophilum*. Only resistance of foliage was detected in *S. berthaultii* and in some accessions of *S. huancabambense* und *S. piurae* from North Peru or Ecuador, *S. andreanum* from Columbia/Venezuela und *S. chiquidenum* from Peru. On the contrary, *S. acaule* and *S. leptophyes* showed resistance only on tubers. Considerable variability of resistance/susceptibility occurred in most species as well as in majority of accessions and depends from location in which the accession has been adapted.

Since 1967 tubers of GLKS grown in greenhouse were systematically (yearly) tested for tuber blight resistance (see 4.4.1.). Accessions with a very high level of resistance (score ≥8 in average of tested genotypes) are listed in table 24, related to series and species. Single genotypes with score 8 can be selected from accessions with lower average value too; however often its stability decreases with lower average. One has to select against susceptibility on the one hand *and* against known and unknown R-genes on the other hand (Parlevliet 1993), but has a chance for success only with the highest possible load of polygenes.

Table 24 Number of highly resistant accessions (score ≥8 in a scale 1-9) of *Solanum*-species to *Phytophthora infestans* in Gene Bank Gross Luesewitz (GLKS, Darsow et al. 2002).

	Foliage blight resistance		Tuber blight resistance	
Series according to Hawkes (1990)	Number of assessed accessions	Number of species with highly resistant accessions	Number of assessed accessions	Number of species with highly resistant accessions
Acaulia	37	0	62	1
Bulbocastana	8	1	29	2
Circaeifolia	4	2	7	1
Commersoniana	10	0	20	1
Conicibaccata	12	1	16	0
Cuneolata	3	0	4	0
Demissa	152	2	190	3
Lignicaulia	1	0	1	-
Longipedicellata	96	3	131	4
Megistacroloba	29	0	83	0
Morelliformia	0	-	1	0
Etuberosa	1	0	-	-
Pinnatisecta	26	0	64	5
Piruana	2	2	1	0
Polyadenia	6	0	7	0
Tuberosa cultivated	508	0	1453	0
Tuberosa wild	113	3	338	4
Yungasensa	62	0	107	0
Sum	1074	14	2514	21

5.2. Use of wild species in pre-breeding for quantitative late blight resistance

According to Huaman et al. (2000) 1,024 accessions from 2,738 tested ones have useful genes for foliage blight resistance. Examples are given of used sources (species) of resistance for some (pre-)breeding programmes and for INCO-PAPA project (1998-2001, European countries and Latin American ones were involved). Species are listed which were used by crossing or fusion in decided late blight programmes independently from positive or negative results of its employment. Following literature is used for the data in table 25: project INCOPAPA (Schilde-Rentschler et al. 2002), pre-breeding and breeding in Russia (Kameraz 1958, 1968, 1971, Kameraz et al. 1974, Kameraz & Patrikeyeva 1980, Kotova 1981, Kameraz et al. 1982, Morozova 1984, Kirsanova et al. 1989), pre-breeding in Mexico (Niederhauser 1962, Rivera-Pena 1990a, 1992, 1999, 2005, Rivera-Pena & Lopez Mateos 2004), pre-breeding in USA (Plaisted et al. 1987, Gundersen et al. 2000, Hayes & Thill 2002, Novy et al. 2005, 2007, Simko et al. 2007, Zarka et al. 2009), breeding in CIP (Annual Reports, Estrada & Turkensteen 1978, Huaman 1982, Mendoza 1987, 1992, Schmiediche 1987, Landeo et al. 1995, 1995/96, Trognitz et al. 1995/96, Perez et al. 2000), pre-breeding in UK (Black 1960, 1964, Holden 1977, Bradshaw et al. 1995a, 2009, Stewart & Ramsay 1999), in Germany (Schick 1932, Lehmann 1937, Stelzner 1949, Rudorf et al. 1950, Oertel 1972, Darsow 1993, 1995, 2000a, 2000b, Darsow et al. 1996, 2002, Thieme et al. 1997, 2005, 2008, 2010, 2011a, b, Smyda et al. 2011).

Table 25 Species (Systematics of Hawkes 1990 and of Bukasov 1973) which are used (+) in pre-breeding for resistance to *P. infestans* in some countries and INCOPAPA project.

Species	INCO PAPA	SU/Russia	Mexico	USA	CIP	UK	GER
S. acaule		+			+		+
S. avilesi	+						
S. berthaultii	+	+	+	+		+	+
S. brachycarpum	+		+				+
S. bulbocastanum	+	+		+	+		+
S. canasense	+						
S. capsicibaccatum	+	+					
S. cardiophyllum		+				+	+
S. catarthrum		+					
S. chacoense		+				+	+
S. chancayense							+
S. chiquidenum	+						
S. circaeifolium	+						+
S. commersonii	+					+	+
S. demissum		+	+		+	+	+
S. x edinense			+			+	
S. fendleri				+			+
S. goniocalyx					+		
S. guerreroense							+
S. gibberulosum		+					
S. hjertingii				+			+
S. hondelmannii	+						
S. hougasii			+	+		+	+
S. infundibuliformae			+				
S. iopetalum			+				
S. jamesii	+				+		+
S. kurtzianum			+				
S. maglia						+	
S. microdontum		+	+	+		+	+
S. molinae		+					
S. okadae	+			+			+
S. papita		+				+	+
S. parodii		+					
S. phureja			+	+	+	+	+
S. pinnatisectum	+	+		+	+		+
S. polyadenium	+	+					+

Species	INCO PAPA	SU/Russia	Mexico	USA	CIP	UK	GER
S. polytrichon		+	+				+
S. rybinii		+					
S. x sambucinum							+
S. sancta rosae		+					
S. semidemissum		+					
S. simplicifolium		+				+	
S. sparsipilum			+				
S. spegazzinii			+				
S. stenotomum		+	+	+	+	+	
S. stoloniferum	+	+	+		+	+	+
S. sucrense	+		+				+
S. tarijense							+
S. tarnii							+
S. toralapanum							+
S. trifidum				+			+
S. tbr. ssp. *andigena*		+	+	+	+	+	+
S. tuquerrense							+
S. vallis-mexici		+					
S. velascanum		+					
S. vernei		+	+				+
S. verrucosum		+	+	+	+	+	+

Mainly insufficiently strong concepts are to notice concerning the exploiting of wild sources of late blight resistance. The level of resistance in potential sources of resistance is only one decisive aspect; selection for long day tolerance (for use in temperate climate) and other traits in the source increases the chance of success in all if polygenic inheritance is used. Of course, cultivated species are to prefer because of lesser expressed undesirable traits and shorter breeding course; however low foliage blight resistance and absence of tuber blight resistance are the rule (Darsow & Hinze 1991a, b, 1992, Darsow et al. 1993). However, a useful quantitative level of foliage resistance in it is repeatedly mentioned (Simmonds & Malcolmson 1967, Mendoza 1987, Glendinning 1989, Haynes & Christ 2006, Gabriel et al. 2007). In general, consideration of aspects of breeding is insufficiently realised in the early stage of pre-breeding for effective increase of quantitative late blight resistance of new cultivars later.

A lot of valuable experience is described in the R-gene area about traits of used species, about problems with fertility, very impeding traits or unexpected additional gain from wild species in potato pre-breeding (Schick & Lehmann 1936, Lehmann 1937, 1938a, 1938b, Propach 1937, Bukasov 1938, Stelzner & Lehmann 1944, Rudorf & Schaper 1951), which is mainly not known or partly repeated detected. Breeding on the level of wild species is recommended to improve sources before first cross with *tbr* in its blight resistance or to use other desired traits at the same time or reduce the expression of undesirable traits (Graham 1963, Kameraz 1968, Kameraz et al. 1974, 1982, Hermsen 1977, Kameraz & Patrikeyeva 1980), but it is not usually. Such step takes time, but reduces the necessary backcross series (Kameraz 1968, Hermsen 1977, Foldø 1987) and/or improves the chance to transfer really enough polygenes to the new variety. Selection for adaptation to long day conditions is in this stage necessary and effectively. On the contrary,

population breeding as in Neo-Tuberosum programmes changes the traits by repeated cycles of self-pollination and selection (Simmonds 1966, 1969, Simmonds & Malcolmson 1967, Tarn et al. 1977, 1990, Mendoza 1979, 1987, Munoz & Plaisted 1981, Plaisted 1987, Plaisted et al. 1987, Glendinning 1989, Haynes & Christ 1999, 2006). However, these programmes are carried out mainly with scientific aim to repeat evolution of *S. tuberosum* ssp. *tuberosum* and not as pre-breeding to prepare best use of new sources in variety breeding. Only few traits were selected for; therefore best clones have had too much negative expressed other traits to be successfully used as parents in cultivar breeding. These programmes mainly are finished because of economical reasons (see chapter 10.3.). At CIP, Lima, population breeding is applied for practical demand of breeding in populations B without R-genes for late blight resistance, and supplemented by clone breeding (Landeo 2002).

Combined resistance on foliage and tubers is frequently not realized in selected sources of resistance. However, each cross step of a resistant parent with a susceptible parent results in dispersal of polygenes for resistance in the progeny and reduced level of resistance. From the literature the impression arose that use of 'new' sources (species) for blight resistance is much more attractively and supported than more qualified choice of best sources in known species and accessions with the intention to solve the highly complex challenge for practical breeding by application of all scientific and practical knowledge and by avoiding all known defects and wrong decisions made in more than 150 years of experiments to exploit wild species. Very high potential would be realized by analysing of disappointing results and improved repetition; both usually does not occur in realizing pre-breeding by succession of short projects with scientific or economic value.

Adaptation of highly late blight resistant interspecific hybrids from the source of resistance to the eco-climatic conditions of the intended area of growing is to conduct by a series of crosses in pre-breeding. The best sources are adapted to short day. In long day poor tuberization, extreme lateness, and very long stolones besides other deficiencies are visible. These polygenic determined reactions show different variation in different species, but mostly breeding and selection on species-level is effectively, for instance in *S. pinnatisectum* (see fig. 73). Required changes in the genome of the first breeding products with high blight resistance are the main task of that pre-breeding.

Crossability of cultivated and wild species with *tbr* is a problem not only because of ploidy levels from diploid to hexaploid, but also because of pre- and postzygotic barriers (von Wangenheim et al. 1957). Male sterility and self-incompatibility are wide-spread; several alleles of sterility are known (Rudorf & Schaper 1951). Many wild species are cross-incompatible with each other as well as with *tbr* cultivars. Autotetraploids and allopolyploids complicate possible crossing. An overview is given by Hermsen (1994) and Hanneman (1999), including cellular and molecular approaches to manage the difficulties. Besides the ploidy level a hypothetical value in the endosperm is to consider, the EBN-number (Johnston & Hanneman 1981, Hanneman & Ehlenfeldt 1984). Some authors are mentioned reporting extensive results of inter-specific crossing including double pollination and embryo rescue (von Wangenheim 1957, von Wangenheim et al. 1957, Bukasov and Kameraz 1959, 1973, Dionne 1961, Grun 1961, Kameraz 1973, Hawkes 1979a, b, Kameraz et al. 1982, Peloquin et al. 1984, Brown 1988, Bamberg 1990, Brown and Adiwilaga 1990, Watanabe et al. 1990, Hamernik et al. 2001). *S. acaule* often is used as bridge to introduce wild species into *tbr* (Dionne 1963, Hermsen & Ramanna 1973). Doubled diploid *S. commersonii* can be used as a bridge species with *S. acaule* or *Longipedicellata* species resulting in F1 hybrids, which directly or after selfing as F2 by unreduced gametes enable crossing with *tbr* (Bamberg et al. 1995). Ploidy/EBN manipulation, bridging species *S. verrucosum* (Abdalla 1970), combining of growth regulator application and embryo rescue have been used to bypass reproductive barriers between Mexican wild species *S. bulbocastanum*, *S. cardiophyllum*, *S. pinnatisectum*, *S. tarnii* and *S. trifidum* with *tbr* by Thill et al. (2003), *S. chancayense*, *S. commersonii* additionally by Jansky et al. (2009b). A review is given by Jansky (2006) how to overcome

hybridization barriers with many successful examples and used combination of methods as ploidy manipulations, bridge crosses, auxin treatment, mentor pollinations and embryo rescue as well as somatic fusions. Inter-EBN interspecific crosses of 1 EBN species with *S. verrucosum* are explained by mutation steps and new results widen the possibilities of practical pre-breeding on diploid level (Yermishin et al. 2011).

A part of breeding to introduce valuable genes from cultivated and wild species is carried out on diploid level, for blight resistance too (Howard 1970, Budin et al. 1978, de Main 1978, 1982, Tiemann 1981, 1991, Swiezynski et al. 1983, Iwanaga 1984, Osiecka 1988, Rivera-Pena 1990a, Bradshaw & Mackay 1994, Ortiz & Peloquin 1994, Hanneman 2000, Wasilewicz-Flis et al. 2000, Jakuczun et al. 2000, 2010, Darsow 2002b), however male fertility of dihaploid clones is generally a limiting factor (Carroll & Low 1976, Hutten et al. 1995, De Maine 1997, Anoshenko & Podlisskikh 2000, Voronkova et al. 2002, Bradshaw 2009), which is stronger in blight resistant clones descend from different species. Higher labour-intensity and some logistic problems additionally hamper breeding on diploid level. Balanced genome and fertility of tetraploid progeny was quicker reached by crossing of *S. demissum* with a diploid parent (Rudorf & Schaper 1951). Production of 2n pollen of resistant dihaploid clones enabled direct crossing with female tetraploid potatoes. However, often tetraploid fusionates as *pnt* + *tbr* continue the cross incompatibility of the wild species. A solution and explanation is given by Yermishin et al. (2002) by producing dihaploids and going on with fertile individuals successfully. Diploid *S. verrucosum* as female parent was successfully crossed with 1EBN species as first step in diploid breeding programmes (Yermishin et al. 2011). Inbreeding depression and self-incompatibility in diploid germplasm and dihaploids has hitherto blocked the development of potato inbred lines. Backcrossing with a homozygous progenitor of the *Sli* gene gave self-compatible offspring from diploid breeding clones (Meijer et al. 2011). This result opens new practical possibilities in potato breeding by using out- and inbreeding.

Biotechnological methods expand the possibilities to use difficult or not crossable sources of resistance for breeding. So Mexican species came broad to exploit as well as by protoplast fusion (Schilde-Rentschler et al. 1993, Darsow et al. 1994, Bradshaw et al. 1995a, Thieme et al. 1997, 2005, Helgeson et al. 1998, Yakovleva et al. 2005, Jakuczun et al. 2010) as by gene engineering, which is focussed on major genes (Song et al. 2003, Van der Vossen et al. 2005, Kuhl & Douches 2007). An example of analysing somatic hybrids of *S. bulbocastanum* with *S. tuberosum* is given by Iovene et al. (2007), in which the chromosomes are identified by molecular markers species-specific, the genomic dosage is determined by GISH, the plastidal and mitochondrial DNA type is analysed. Such knowledge enables selectively marker-assisted introgression (Debener et al. 1991, Bradshaw et al. 2006c). Chromosome instability *in vitro* is a problem concerning unintentional change, but can be a chance of breeding too (Wilkinson 1994).

Marker-assisted selection (MAS) for quantitative blight resistance in breeding would be very helpful as is discussed in chapter 2.7., but molecular markers operating reliable in a wide gene pool are not enough developed. In the EU project BIOEXPLOIT gene bank material was tested to identify QTL for quantitative foliage blight resistance on chromosome IV, V and X with new SNP markers besides major genes (Hoekstra 2009). Resistance gene enrichment methods have been developed for identifying new R-genes in gene bank material (Verweij et al. 2011a). The development of markers for quantitative resistance has to continue in parallel with improved methodical evaluation of foliage blight resistance (2.5., 2.7, 4.2.4.). Marker-assisted introgression offers the possibility of faster progress than can be achieved by traditional backcrossing. Dale and Bradshaw (2006) give an example for resistance to *Globodera* and a gain of 20 years. However, the target trait is simple inherited and quick examined, all the other traits (linkage drag) be left extensively out of consideration. That is the possibility of research at the moment. In case of using wild material as sources such focussing on one or few simple traits is far from needs in breeding practice and rarely a helpful contribution. Marker-assisted identification of

hybrids can be expected more rapidly which supports donor clone selection not only in back-cross systems (Schweizer et al. 1993, Masuelli et al. 1995, Miraglia et al. 2010).

Only for monogenic determined traits introgression assisted by molecular markers is applied in breeding today. New R-genes are increasingly introduced in potato by protoplast fusion or crossing assisted by molecular markers (Trognitz et al. 2005, 2010, Bradshaw et al. 2006c, Gebhardt et al. 2006, Sliwka et al. 2006a, Carrasco et al. 2009, Hein et al. 2009, Hoekstra 2009, Lokossou et al. 2009, Zarka et al. 2009, Lopez-Vizcon & Ortega 2011, Mahadour et al. 2011, Rogozina et al. 2011, Smyda et al. 2011, Thieme et al. 2011b, Tomczynska et al. 2011, Verweij et al. 2011a).

5.3. Choice of sources for resistance to *P. infestans* at IK, later ILK or ZL Gross Luesewitz

The yearly assessment of blight resistance of GLKS by the group of ZL responsible for potato pre-breeding to late blight resistance included the synergistic effect of using remained tubers of resistant clones for growing and testing a second year as well as for multiplication. Often a third year followed with growing in field assessment for foliage blight resistance parallel to multiplication in greenhouse and selection as cross parent.

It occurred that in one year more than 100 accessions of *S. demissum* were sown in the gene bank. In the fourth year sources of resistance were selected from these (Darsow 2000b). Up to 1,400 wild clones were grown and tested yearly grown from seeds and from tubers. Besides foliage and tuber blight resistance other traits as size of tubers, depth of eyes, length of stolones (fig. 72), intensity of flowering, male fertility, infection with viruses, resistance to nematodes are considered for selection of potential sources of blight resistance. Often more clones were discarded because of these other traits than because of too low level of blight resistance on foliage or tubers (Darsow 1995, Darsow & Schueler 1998). Figure 73 shows the genotypic differences in stolon development between clones of *S. pinnatisectum* as an example for chance of breeding progress on level of wild potatoes. Table 26 informs about the number of grown and tested wild material in second and following years of testing in the period 1984–1999 for selection as cross parents. Of course the main part was discarded before crossing due to imperfection of tubers, too low level of blight resistance, virus infections, and lack of flowering. For instance in 1995 48% of planted wild clones were discarded before second tuber blight assessment. Among the 304 clones tested in 1995 eight percent were scored 9, 30% had score 8, 21% score 7, 16% score 6, other score 5-3. Last two columns in table 26 note seedlings of crosses of wild species with *S. tuberosum* ssp. *tuberosum* (two species) or such as (*S. demissum* x *S. verrucosum)* x *S. tuberosum* ssp. *tuberosum* (= *tbr*) with three species. The cross *dms* x *ver* should promote balanced tetraploid genome and earlier occurrence of mail fertility. The same effect may be reached with *dms* x *tbr* dihaploid (pedigree 3). Combining of different polygenes for resistance was another point of view for interspecific crosses (table 26) and pedigree 1 on page 135. Not as yet it is possible to ascertain whether different accessions or species possess functionally different polygenes for blight resistance. As that is methodically easier to decide for R-genes several cases of synonym effects (orthologous genes) are described (Hein et al. 2009).

Table 26 Investigation of wild and cultivated *Solanum*-species of GLKS and of seedlings of crosses of potato species (F1) for blight resistance (Darsow & Hinze 1991b, Darsow 2000a).

	Number of investigated			clones of own crosses of	
Year of assessment	Wild species	Accessions of GLKS	wild clones of GLKS	2 species	3 species
1984	53	291	506	560	167
1985	44	189	342	636	135
1986	56	171	259	348	87
1987	49	171	249	207	46
1988	42	129	175	575	50
1989	38	157	236	493	61
1990	44	188	319	422	79
1991	35	142	351	487	94
1992	24	63	286	413	107
1993	70	95	281	316	53
1994	37	67	377	264	114
1995	27	98	304	298	146
1996	37	72	360	325	139
1997	18	84	203	282	151
1998	40	91	293	248	133
1999	21	60	190	219	79

5.4. Use of wild species in pre-breeding for quantitative blight resistance at ZL Gross Luesewitz, pedigrees and additional information

Specialized pre-breeding for quantitative blight resistance was started at Gross Luesewitz in 1964 separately from cultivar breeding. We hoped to find potential sources of blight resistance in cultivated species, which should take a shorter breeding way up to new cultivars, but genotypes of this group contributed rarely and only little to effective parental clones in pre-breeding, and only combined with sources from wild species.

First sources of resistance were *Solanum demissum* (*dms*) number 1947, Reddick 52.20.154 and PI 160.227 (see fig. 71). In our climatic conditions only in greenhouse very little tubers were developed (fig. 74), not in the field. The size relation of biggest *dms*-tubers to a middle *tbr*-tuber (fig. 75) makes imagible the back-stroke of outcome of first cross with *tbr* concerning yield, tuber size and most other cultural traits (see fig. 72). The progeny from crosses (seedlings) were grown in greenhouse; from second year the progeny was grown in the field. As much as possible traits were observed for following four years and the best clones used for crossing (fig. 76-78). This procedure was repeated up to backcross two (BC2) or three (BC3) to return from wild to nearly cultivar level (see fig. 72). Missing male fertility of BC-clones gave no alternatives.

Plants *dms* have three genomes, they are considered to be most likely homologous or highly homologous to AA and nearly autoploid (Pedinen et al. 20111). In its use became apparent that the level of resistance fell down quicker than the traits of highest interest could be improved. And this tendency occurred although used German cultivars shared a relatively high portion of genes from *S. demissum* in international comparison (Ross 1986). We had to cross resistant

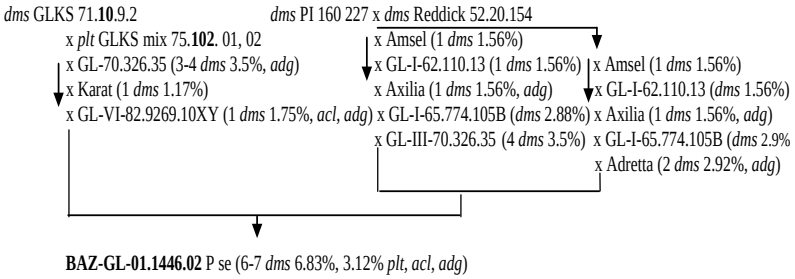
x resistant. Lack of male fertility and susceptibility to virus diseases made it difficult. New, different sources of blight resistance had to be selected for combining of resistance. For instance in *S. stoloniferum* was searched for male fertile plants with late blight resistance. Such clones were discovered (fig. 79) and they enabled successful to go on (fig. 80). Due to selection of additional sources of resistance with advantages and disadvantages in different traits more intercrossing was possible with expected diverse resistance. Since 1998 selection of new sources was reduced in favour of progressed material of BC4. However, continuously introduction of genes for resistance from not related donors is necessary to remain a sufficient broad basis in pre-breeding 20 years later, in future.

Our strategy included

1. use of taxonomically and geographically different species and accessions to breed on a genetic very broad basis on diploid and tetraploid level.
2. beginning with combined foliage and tuber resistance near score 8 in the source of resistance.
3. starting with selfing or crossing on wild level in or between accessions of a species or between species to improve the wild parent and to accumulate different polygenes for blight resistance and to improve other traits at the same time.
4. considering so many traits as possible for selection before production of F1 with *tbr*.
5. use of protoplast fusion and embryo rescue besides conventional breeding.

Pedigrees are given in a simplified manner showing only the succession of crosses. The cross parents are written one beneath the other in chronological order according the arrow. As common practice the female parent is written first (on the left), the male parent on the right. That means, in succession the male parents are mentioned and the female is selected from the cross before. If there was an exception and the mentioned parent was used as female one, the sign ♀ follows the clone name; then the male parent is selected from the cross before.

Pedigree 1:



Pedigree 1 gives an example of a pre-breeding clone in which new sources are introduced. On the left side a succession follows a cross of *dms* (10) from gene bank GLKS Gross Luesewitz, accession 9, plant 2 with pollen of *plt* (species number 102) from several genotypes of accession 01 and 02 as mix. One clone from the progeny is crossed as female parent with clone GL-III-70.326.35 as pollinator. Obtained seeds of this cross were sown and again one clone of it was used as female parent to be pollinated with cultivar Karat. In this manner the cross parents are written one beneath the other in chronological order used as pollinator to the female parent selected from the preceding cross. Behind clone GL-III-70.326.35 (3-4 *dms* 3.5%, *adg*) is written, which means 3-4 different clones *of dms* are involved in the pedigree of GL-III-70.326.35 with a calculated part of 3.5% of its genome assuming accidental distribution in meioses of all pre-

ceding cross steps. The probable percentage of *dms* or other sources of late blight resistance is calculated from available pedigree information (IK Gross Luesewitz, Norika Gross Luesewitz, Swiezynski et al. 1997c, van Berloo et al. 2007). Because of missing information in cases of cultivars Berezka, Dunja, Dorett, Panda, Pamir and Tessi in other pedigrees plausible assumption were used. From additional existing genomic parts of *adg* in GL-III-70.326.35 a contribution to late blight resistance is not expected, therefore its part is not calculated, but mentioned. Similar the short information to other cross parents in brackets is to understand. Among cultivated cross parents such are preferred with lesser late blight susceptibility or helpful resistance as in GL-III-70.326.35. Already pedigree 1 shows that use of some cultivated clones with a genomic part of about 3% *dms* can effectively contribute to increased level of late blight resistance. Which level makes the difference between backcrossing and inter-crossing?

From the cross *dms* x *dms* on the right side with the name of its accessions two cross successions go on which differ only in the last step. Thereafter follows an intercross resistant x resistant, from which a pollinator was selected to combine the three successions and from which clone BAZ-GL-01.1446.02 was selected. After the clone number 'P se' is written. P means high late blight resistance on foliage and tubers; se indicates second early maturity. In general, combinations of 2-3 letters each following the clone number roughly characterize beneficial traits and are explained as abbreviation of *Solanum species* (*dms, plt*) in "Abbreviations used", page 261-262. BAZ-GL-01.1446.02 could possess genes from 6-7 different *dms*-clones on probably 6.83% of its genome; one *plt*-clone accounts for 3.12% of the genome; *acl* and *adg* are also included. Different polygenes for resistance are brought together by inter-crossing. Parent GL-VI-82.9269.10XY with extreme resistance to PVY and PVX was used to produce BC2 with improved virus resistance.

Table 27 Seedlings percentage in classes of foliage and tuber blight resistance assessed in first year of cultivation in greenhouse. Introduction of new sources of resistance from *S. demissum* (10. .). Scale 1-9 with increasing resistance.

		Foliage blight resistance			Tuber blight resistance	
Cross	Parents score	5	6-7	≥8	aver-age	% with ≥7
1	10.9 x *S. polytrichon* (*plt* mix)	0	3	97	8.4	86
2	(10.9 x *plt*) x Karat	24	29	47	4.6	2
3	10.9 x *S. tbr* ssp. *andigena*	1	27	72	7.5	65
4	10.9 x *S. caldasii* syn. *chacoense* , *chc*	0	1	99	8.6	90
5	(10.9.2 x *chc*) x GL-III-70.326.35	13	28	59	5.1	8
6	(10.9.5 x *chc*) x GL-III-70.326.35	15	17	68	5.9	16
7	10.9 x GL-III-70.326.35	2	33	65	7.7	80
8	10.8 x GL-III-70.326.35	4	22	74	6.6	25
9	10.z x *S. stoloniferum*	0	5	95	6.7	38
10	10.z x *tbr dihaploid*	0	4	96	7.8	73
Standard population, Adretta open pollinated		11	0	3.2	0	0

Until 1992 24 different accessions of *S. demissum*, 10 of *S. stoloniferum*, one each of *S. papita*, *S. verrucosum*, *S. hougasii*, *S. hjertingii*, *S. fendleri*, *S. tarijense*, *S. chancayense*, two of *S. mochiquense*, three of *S. toralapanum*, one of *S. tuquerrense*, two of *S. bulbocastanum*, three of *S. tuberosum* ssp. *andigena* were started to use in pre-breeding programme by crossing (Darsow 1993). Usu-

ally several different genotypes of an accession are crossed, sometimes a mix of pollen even of different accessions was used (see pedigree 1).

Some results of foliage and tuber blight resistance are shown from first cross steps to introduce new sources of resistance in the pre-breeding programme (table 27). Clones of *S. demissum* are crossed with tetraploid or diploid cross parents and show different resistance level in the progeny.

Only a small part of these potential sources led to parental clones of BC4-BC5 because of high susceptibility to virus diseases, low fertility, or too low heritability of blight resistance, negative combining ability, or too negative expression of other traits. Only a broad basis of very diverse breeding material offers the chance to recombine polygenes for blight resistance and other traits. For that after backcross two (BC2) inter-crossing (resistant x resistant) is necessary. Its part for the most important species in 1994 is shown in table 28 (Darsow 1995).

Table 28 Diversity of pre-breeding material for resistance to *Phytophthora infestans* at ILK Gross Luesewitz and its stage of breeding in 1994. (BC6 = backcross 6, [1]: crosses with following number of different species in summary of diverse progenies).

Wild species	Number of used		Manner of the cross		
	Accessions	Genotypes	Backcross	Intercross	Cross of species[1]
S. demissum	17	720	up to BC6	53 %	18
S. stoloniferum	10	328	up to BC5	27 %	19
S. polytrichon	2	68	up to BC2	6 %	4
S. papita	3	29	up to BC2	0 %	2
S. verrucosum	2	119	up to BC1	0 %	3
S. bulbocastanum	6	258	up to BC2	0 %	2

The part of inter-crosses shows the intention to accumulate polygenes for resistance and select against unwanted expression of other traits at the same time in such progeny. We preferred inter-crosses to selfings, which were used by Rudorf (1950). Fertility plays an important part in it (fig. 81). Altogether, 18 different species were crossed with S. demissum-clones at that time, with S. stoloniferum 19 species. A clone of the cross (dms x sto) presents the haulm type (fig. 82), whilst tubers from the cross ((dms x sto) x Kardent) are shown in figure 64. The architecture of the haulm of wild clones differs from tbr by number and stability of stems, size of leaflets and other traits (fig. 83).

Partly selfing or crossing of wild clones with other accessions of the same species or other species preceded first cross with *tbr* to improve resistance or reach desired ploidy level. The following pedigrees represent examples for the three crossing types: in the first step: cross of species, inter-cross resistant x resistant, cross with *tbr* followed by backcross to *tbr*. Pedigree 2.1. showes in very early stage of crossing succession a *tbr*-partner with extreme virus resistance to PVX and PVY and expressed clearly its utilization for starch. The example for inter-cross also shows early its usability for starch, traced back to *dms*-clones and supported by *tbr*-parents. The pedigree 2.2. seems to continue as backcross, but the cross with cvs. Rebecca and Kardent, both can be understood as inter-cross and example for successful application of our strategy. In clone BAZ-GL-99.7933.03 suitability for table potato quality was expressed in hopeful manner in spite of high percentage of *dms*-genome part, which did rarely occur in such early breeding stage; high susceptibility to virus diseases was a problem. Both, the wild donor and selected BC1-clone are shown in figure 84. For the letters following the clone number see "Abbreviations used", page 261-262.

Pedigree 2:

1. Cross of species
dms GLKS 83.**10**.60.4 x *sto* GLKS mix of **22**.2, 3, 6, 22, 24
x GL-VI-82.9269.10XY (1-2 *dms* 1.75%, *acl*, *adg*)
↓
BAZ-GL-93.7024.44 P St (25%) (2-3 *dms* 25.88%, 1 *sto* 25%, *acl*, *adg*)

2. Inter-cross
dms GLKS 83.**10**.20.3 x *dms* GLKS mix of **10**.2, 8, 9, 10, 17, 43, 60, 90, 105
x Rebecca (2-3 *dms* 5.66%, *adg*, *cmm*, *mag*)
x Kardent (2 *dms* 3.12%, *phu*, *vrn*)
↓
BAZ-GL-01.1331.03 P St (24.8%) Ro1, 2, 3, 5 se-sl (2-3 *dms* 27.98%, *adg*, *cmm*, *mag*, *phu*, *vrn*)

3. Backcross
dms GLKS 85.**10**.171.4 x GL-I-78.371.31N (1 *dms* 2.54%, *adg*)
x Rebecca (2-3 *dms* 5.66%, *adg*, *cmm*, *mag*)
↓
BAZ-GL-99.7933.03 P Sp Ro1, 2, 3, 5 se (3-4 *dms* 28.04%, *adg*, *cmm*, *mag*)

In case of using quantitative late blight resistance breeding success depends more on the system of breeding and selection than on single sources of blight resistance. The balance between loss of resistance and gain on other traits is the key for success, not the speed to get cultivar level in few traits. Inter-crossing intended to collect more different polygenes and use additive effects and specific gene interactions for late blight resistance. If adg-clones were introduced crosses with best inheritors of tuber blight resistance had to be used in the next step. The main problem is the 'wildness' of progeny with high part of wild genome. In the R-gene era of breeding for monogenic dominant inherited late blight resistance after crossing dms with tbr (F1) and selection of best few clones followed 3-5 times crossing of best and resistant outcome with tbr in succession (BC1-BC5) with strong selection for all the other traits between the 50% resistant progeny. In this way clones of BC2 could be selected, which look similar potatoes rather than herbs (Schick 1934). BC3 could be near variety level in some important traits (Schmidt 1933, Reddick & Peterson 1947: cultivar Ashworth). That is possible for polygenic resistance type only more slowly, which does not afford such strong selection.

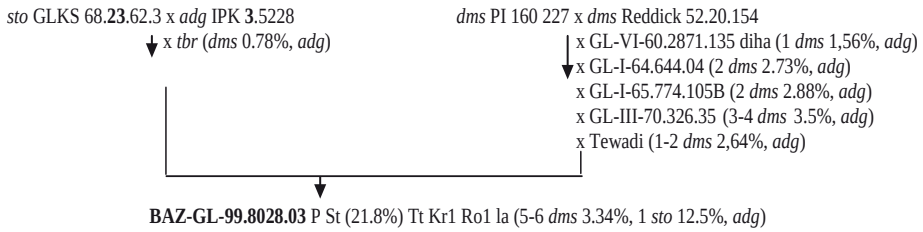
In 1997 33 accessions were new or repeated introduced into a selection cycle of our pre-breeding by sowing, growing in greenhouse, selection for foliage and tuber blight resistance and other traits. Two years later 271 clones from 139 cross combinations were remained from it and grown in the field as A-clones with nine plants each (table 29). It is written, which breeding stage was reached between F1 and BC3 with how many cross combinations. Genetic diversity of resistance is supported by crosses resistant x resistant, respectively BC x BC. Sometimes species additionally were crossed with each other before backcrossing. Therefore table 29 informs about the number of blight-resistant species, which were included by the cross combinations with each of the accessions. For instance, in case of d*ms* GLKS 10.08 in first line two combinations included one resistant species (crossed with *tbr*) and one combination with two wild species. One of these combinations corresponds with first cross with *tbr*: F1, two other with the first backcross: BC1 = ((species x cultivar) x cultivar)). "*Sto* å of 7 accessions 23" means pollen mix of seven accessions of species-number 23 of GLKS, *S. stoloniferum* was used.

Table 29 Cross combinations grown 1999 in the field as A-clones descend from new accessions. The number of species combined with that accession and its cross step. BC = backcross. Species: *dms* = *S. demissum*, *hjt* = *S. hjertingii*, *pta* = *S. papita*, *ver* = *S. verrucosum, sto* = *S. stoloniferum*, *plt* = *S. polytrichon*, *crc* = *S. circaeifolium, adg* = *S. tuberosum* ssp. *andigena*.

Species and accession	Number of cross combinations including following number of blight-resistant species				Cross step of grown clones including the written accession				
	1	2	3	4	F1	BC1	BC2	BC3	BCxBC
d*ms* GLKS 10.08	2	1	-	-	1	2	-	-	-
d*ms* GLKS 10.09	6	6	-	-	3	5	-	-	4
d*ms* GLKS 10.10	-	3	-	1	2	1	-	-	1
d*ms* GLKS 10.11	-	1	1	1	1	1	-	-	1
d*ms* GLKS 10.17	-	1	-	-	1	-	-	-	-
d*ms* GLKS 10.20	10	1	-	-	3	6	-	-	2
d*ms* GLKS 10.43	3	1	-	-	1	3	-	-	-
d*ms* GLKS 10.60	-	8	-	-	8	-	-	-	-
d*ms* GLKS 10.90	-	1	-	-	1	-	-	-	-
d*ms* GLKS 10.105	2	-	-	-	2	-	-	-	-
d*ms* GLKS 10.?	2	5	1	-	6	2	-	-	-
dms ∑ 8 accessions	1	1	-	-	2	-	-	-	-
hjt GLKS 145.2	-	1	-	-	1	-	-	-	-
hjt GLKS 145.4	-	1	-	-	-	-	-	1	-
pta GLKS 136.2	1	-	-	-	1	-	-	-	-
pta GLKS 136.4	-	2	-	-	-	1	-	-	1
ver GLKS 40.2	-	1	-	-	1	-	-	-	-
ver GLKS 40.4	-	1	-	-	1	-	-	-	-
sto GLKS 23.60	-	1	-	-	1	-	-	-	4
sto GLKS 23.63	-	1	-	-	1	-	-	-	-
sto GLKS 23.84	-	1	-	-	1	-	-	-	-
sto ∑ of 7 accessions 23	4	3	-	3	1	1	-	2	-
sto ∑ of 7 accessions 22	2	5	-	-	7	-	-	-	-
plt Petersburg		2	-	-	-	2	-	-	-
crc BGRC 27034	7	-	-	-	-	-	-	-	7
blb BGRC 08006	3	-	-	-	-	-	2	-	1
blb K 4207 Petersburg	1	-	-	-	-	-	-	-	1
blb ABPT Wageningen	-	3	4	9	-	-	3	-	13
pnt K 2503-1 Petersburg	-	1	-	-	-	-	-	-	1
pnt GLKS 71.06	-	-	-	1	-	-	-	-	1
pnt BGRC 08168	-	3	2	1	-	-	-	-	6
adg IPK 3.5228	-	1	4	-	1	-	-	-	4
adg GLKS ∑ of 6 accessions	-	9	1	1	9	-	-	-	2

Table 29 gives an impression of diversity, complexity and long standing of pre-breeding for resistance against *P. infestans* on the basis of polygenes. Combination of different polygenes for resistance does not hinder from combination of polygenes for resistance with such for quality and yield at the same time (pedigree 3).

Pedigree 3:



Pedigree 3 shows a relatively wild blight resistant clone (P) from *dms* and *sto* suitable for starch (St), tolerant to drought (Tt) and resistant to *Synchytrium endobioticum* race 1 (Kr1) and to *Globodera rostochiensis* pathotype 1 (Ro1) and is late maturing (la). The adg-clone little contributed to late blight resistance, but more to high yield.

Clones of F1 and BC1 in the field develop their haulm more slowly and lesser luxuriantly than *tbr*-material (fig. 85). Good foliage growth is in these examples better combined with suitability for table potato than earlier. *S. papita* is used as new source of late blight resistance (fig. 86).

Up till 2007 197 accessions from 42 species and synonyms entered into pre-breeding of ZL Gross Luesewitz. Most frequently exploited ten species so far are listed in table 30. The boldface number following GLKS is the species number of the system, normal numbers mean the accession. Other gene banks have other systems.

Table 30 Most frequently used species in pre-breeding for late blight resistance at ZL Gross Luesewitz

Species	Species	Accessions
S. demissum	GLKS **010**.	3, 4, 5, 6, 8, 9, 10, 11, 12, 15, 17, 20, 24, 26, 29, 30, 31, 34, 39, 40, 41, 42, 43, 44, 46, 48, 59, 60, 61, 78, 79, 81, 82, 85, 86, 89, 90, 105, 121, 136, 139, 140, 146, 147, 152, 160, 162, 164, 171, 173, 174, 181.
		PI 160227, Reddick 1952.20.154, 1947RRR.
S. stoloniferum	GLKS **004**. GLKS **022**. GLKS **023**.	16, 19. 1, 2, 3, 6, 11, 22, 24. 4, 6, 50, 52, 60, 62, 63, 65, 76, 79, 84.
		BGRC 7230, 2490-5 from Saint Petersburg.
S. hougasii	GLKS **144**.	1, 7, 8,
S. polytrichon	GLKS **102**.	2, 5, 9,
S. hjertingii	GLKS **145**.	2, 3, 4, 7, 12,
S. circaeifolium		BGRC 27034.
S. okadae		BGRC 028969, BGRC 028970.
S. sucrense	GLKS **033**.	16, BGRC 27370.
S. bulbocastanum	GLKS **088**.	38, 40, 43, 44, 46.
		H-1983, H-1588-23 as ABPT from Wageningen.
		BGRC 008006, K-4207 from Saint Petersburg.
S. tuberosum ssp. *andigena*	GLKS **003**.	209, 379, 982, 1453, 1457, 1569, 1574, 1693, 1797, 1815, 1835, 1952, 2077.32, 2115.025228.
		CIP 702299 and more from CIP with unknown descent.

Selected potential sources of late blight resistance should possess resistance on foliage and tubers and additionally as possible other desired traits as for instance extreme resistance to PVY (Thieme et al. 2005) or quality traits (Hayes & Thill 2001). The introduction of the resistance genes follows stable establishing in the genome of cultural potato parallel with re-establishing quality, yield, earlier maturity and a lot of other traits stepwise, which are mainly lost in first cross with wild donor. This process of drastic reconstruction to replace all undesired 'wild alleles' in F1 has been driven to a breeding stage near backcross four (BC4) in pre-breeding. If a broad genetic basis exists, there are many possibilities of crossing BC2 x BC4, (BC2 x cultivar) x BC3, BC3 x BC5 or similarly to improve traits in pre-breeding stock without loss of late blight resistance. Additionally continuously new sources of resistance are exploited in small extent.

5.5. Broadening of genetic basis of blight resistance by using sources of series *Bulbocastana*, *Pinnatisecta*, *Circaeifolia* and other by protoplast fusion or crossing

S. bulbocastanum (*blb*) belongs to the few species 'immune' to late blight according to Reddick (1934). It's very high level of field resistance is confirmed by Niederhauser (1991); however none of the tested tuber-bearing *Solanum* species proved to be immune. Own attempts conventionally to use distant relative wild species of potato as *blb* did not led to introduction into *tbr* genome. Nevertheless, after doubling with colchicine F1 and BC1 with tetraploid *tbr* was succeeded (Livermore & Johnstone 1940, Lebedyeva 1966, Zhitlova 1969, 1982), the same

procedure resulted in hybrid progeny with *pnt*, *cph* and *trf* (Zhitlova 1969, 1971). Sexual hybrids of dihaploids from *tbr* x *pnt* and *adg* x *pnt* could be used by Yermishin and Khlebnikova (2002) as females to produce (*tbr* x *pnt*) x *tbr* hybrids with a self-compatible highly male fertile 2n*tbr*. Hamernik et al. (2001) described formation of a *pnt-tbr* dihaploid hybrid using double pollination and embryo rescue. Another way is used by bridge-crossing (Dionne 1963, Hermsen & Ramanna 1973, Hermsen 1977, 1983, 1994, Bamberg & Hanneman 1986, Bamberg et al. 1995, Hamernik et al. 2001, Thill et al. 2003). Both outcome was compared (Darsow et al. 1996) and showed the problem of disturbed meiosis and preferred loss of desired resistance with parts of *blb* genome as confirmed by Masuelli et al. (1995), Oberwalder (1996) and Boltowicz et al. (2005). Podgayetskiy (1981) crossed *blb* with *dms* followed by *adg* or *tbr* or used ABP according to Hermsen and Ramanna (1973) and showed that repeated crossing can have success. Other bridges are *S. verrucosum* (Abdalla & Hermsen 1973, Thill et al. 2003, Yermishin et al. 2011) and *S. commersonii* (Bamberg & Hanneman 1986, Bamberg et al. 1995). Sidorov et al. (1994) used only the chloroplast and mitochondrial gene pool of *S. bulbocastanum* and *S. pinnatisectum* by protoplast fusion. Protoplast fusion of *blb* (selected diploid plant of BGRC 008006) with dihaploid *tbr* led to successful addition of both genomes by electro-fusion at the University of Tuebingen (Schilde-Rentschler et al. 1993, Oberwalder 1996, Oberwalder et al. 1998) in co-operation with ZL (Darsow et al. 1996, 1997, Darsow 2008). The wild alleles of *blb* were dominantly expressed in fusions as well in resistance as in maturity and most tuber traits (comparison of the first and last column of table 31). Concerning blight resistance on foliage (field assessment with maximal known pathogenicity of inoculum) and tubers (slice test) this result was desired. However, expression of most other traits means a huge breeding challenge.

Table 31 Average of symmetric fusions of diploid S. *bulbocastanum* (*blb*) and dihaploid *S. tuberosum* (*tbr*) B15, combination 6979 and its fusion partners in two years field assessment at Gross Luesewitz. x_F: mean value of fusions; s: standard derivation; n: number of clones; x_P: mean value of fusion partners; Δ years: difference between years. Scale 1-9 with best expression in 9.

	Fusions						Partners of fusion		
Trait	x_F	s	Δ years	Max	Min	n	blb	tbr	x_P
Foliage blight resistance	8.6	0.1	0.1	8.8	8.6	68	8.8	1.6	5.2
Tuber blight resistance	8.4	0.2	0.1	8.7	7.9	68	8.6	4.6	6.5
Early development of foliage	3.0	1.4	0.50	5.0	1.0	66	3.0	5.0	4.0
Maximal haulm development	4.3	2.0	0.77	8.0	1.0	66	2.0	3.5	2.8
Intensity of flowering	4.8	2.7	1.11	9.0	1.0	60	4.0	2.5	3.2
Set of berries	1.0	0.3	0.01	3.0	1.0	59	1.0	1.0	1.0
Deformation of leaves	7.2	1.3	1.15	9.0	3.0	60	9.0	9.0	9.0
Maturity	1.1	0.3	0.17	2.0	1.0	61	1.0	4.0	2.5
Yield (g/plant)	582	452	243	2200	0	63	2.5	353	178
Size of tubers	3.5	2.2	0	8.0	1.0	64	1.5	3.5	2.5
Overall-impression of tubers	2.5	1.3	0.2	4.5	1.0	66	1.5	5.5	3.5
Depth of eyes	5.2	0.8	0.4	6.0	3.0	48	4.5	8.0	6.2
Beauty of tubers	3.5	0.8	0.2	4.5	1.0	48	4.0	7.2	5.6
Deformation of tubers	3.1	1.4	0.3	5.0	1.0	48	8.0	9.0	8.5
Colour of tuber flesh	4.0	0.9	0.3	5.0	3.0	14	1.0	7.0	4.0

Very slow juvenile development of haulm was followed by luxurious growth of haulm later on (fig. 87). Anomalies of leaves occurred often and set of berries was rarely observed. The wild fusion partner caused extreme lateness. Haulm mass, size of tubers and yield were more influenced by change to tetraploid level than by performance of partners. During decades of pre-breeding never such deformed tubers were seen before. About 10 % male fertile clones and below 1% female fertile ones were found. Therefore Hermsen (1977) concluded genes for other desired traits are easier to transfer from other species.

Asymmetric fusion intended to introduce only a fragment of wild species genome. Desired resistance should be expressed with reduced drawback for cultural traits compared with symmetric fusion. For that protoplasts of the wild partner were irradiated with X-rays of 3.5 gy/minute up to two hours before fusion (Oberwalder 1996). Comparison of symmetric and asymmetric fusion of *blb* + BP1076 is given in table 32.

Table 32 Comparison of 2-4 years expression of traits (1-9) in symmetric (7261) and asymmetric fusion (7260) of diploid *S. bulbocastanum* (*blb*) und dihaploid *S. tuberosum* ssp. *tuberosum* (*tbr*) BP1076. x_F: mean value of fusions; s: standard derivation; n: number of clones; x_P: mean value of fusion partners.

Statistic parameter	Foliage blight resistant	Tuber blight resistant	Maturity	Haulm-mass	Intensity of flowering	Yield (g/plant	Tuber impression	Tuber size	Tuber defects	Colour of tuber flesh	Starch content (%)
	Symmetric fusion										
x_F	8.8	6.2	1.6	3.5	4.6	310	2.7	4.5	3.0	1.9	15.5
s	0.1	0.5	0.5	1.2	2.0	231	1.0	1.9	0.7	0.4	1.7
n	14	14	14	14	14	14	14	14	14	8	4
	Asymmetric fusion										
x_F	5.4	4.6	2.7	3.3	4.6	338	3.7	4.2	3.3	2.6	18.1
s	2.5	0.9	0.8	0.9	2.5	264	0.7	1.3	1.2	0.4	2.5
n	23	23	23	23	23	23	23	23	23	21	17
	Partners of fusion										
blb	8.9	8.2	1.0	2.0	5.0	9	1.5	2.0	3.0	1.0	--
tbr	3.4	4.3	3.5	4.0	1.7	566	5.5	4.0	6.0	5.5	16.4
x_P	6.1	6.2	2.2	3.0	3.4	288	3.5	3.0	4.5	3.2	--

Comparison of mean value of fusions (x_F) with midparent value x_P shows often distinct deviations. In symmetric fusion wild type foliage resistance level is expressed, whilst on tubers expected midparent value is realized. Maturity and intensity of flowering of fusion products also coincide with *S. bulbocastanum*.

Asymmetric fusion of *blb* with dihaploid *tbr* caused higher variability of most traits and reduced 'wild effect' compared with symmetric fusion. However, irradiation of *blb*-partner led to loss of important or most genes for blight resistance, on tubers more clear than on foliage. The same was stated also in other combinations. Additional disadvantages were lesser regeneration rate and much reduced fertility. Rarely a cross parent could be selected from asymmetric fusions (pedigree 4, table 32).

Pedigree 4:

Cultivar Regina (1 *dms* 1.02%, 1 *sto* 0.78%, *acl*, *adg*, *spg*) + *blb* BGRC 008006
↓ Selfing
↓
B**AZ-GL-99.7866.01** P Sp se-sl (1 *dms* 0.68%, <20% *blb*, *acl*, *adg*, *spg*, *sto*)

Hanneman and Ramon (1999) have obtained full resistance to late blight even in BC3 in their conditions. Marker-based selection allowed effective transfer of RB-gene (hypersensitivity) into potato using backcross after fusion (Colton et al. 2006). In our use of *blb* the level of blight resistance frequently dropped down in backcross generations because of preferred loss of wild genome parts. BAZ-GL-01.1336.01 was a clone which traced back to *blb*-fusion but without enough improved quality traits (see fig. 65). Absence of table potato quality often was found (fig. 88). Use of sources of *blb* with *Rpi-blb1* and *Rpi-blb3* is continued by Thieme et al. (2011b).

Pedigree 5 for BAZ-GL-03.5119.01 gives an example for using *blb* by bridge crossing only in combination with sources of *dms*. An own cross succession on the left was combined with AB-PTT (Hermsen & Ramanna 1973) from Hermsen, Wageningen, on the right, continued by crossing with cultivar Salomé. BAZ-GL-03.5119.01 was selected from the progeny, possessing late blight resistance on foliage and tubers (P), suitable as table potato (Sp), tolerant to drought (Tt), resistant to potato canker type 1 (Kr1), golden nematode pathotype 1 (Ro1), early to second early maturing (e-se). This clone probably contains genes from 5-6 different clones of *dms* with a calculated part of 2.44%. The part of *S. bulbocastanum* is not calculated because of known preferred losses. Other involved species are *Solanum acaule*, ssp. *andigena*, *S. phureja*. Please look on page 261-262 for explained abbreviations.

Pedigree 5:

dms PI 160 227 — x *dms* Reddick 52.20.154
↓ x Amsel (1 *dms* 1.56%)
↓ x GL-I-62.110.13 (1 *dms* 1.56%, *adg*)
x Axilia (1 *dms* 1.56%, *adg*)
x GL-I-65.774.105B (2 *dms* 2.88%, *adg*)
x GL-III-70.326.35 (3-4 *dms* 3.5%, *adg*)

acl x *blb*
↓ doubled with cholchicin
↓ x *phu*
x *tbr*
x Arkula (1-2 *dms* 2.00%, *adg*)

↓ x Salomé (1-2 *dms* 1.45%, *adg*)
↓
BAZ-GL-03.5119.01 P Sp Tt Kr1 Ro1 ea-se (5-6 *dms* 2.44%, *acl*, *adg*, *blb*, *phu*)

One clone of *S. pinnatisectum* BGRC 08168 was selected as partner for fusion by Schilde-Rentschler at Tuebingen (Menke et al. 1996). About 75% of the somatic hybrids were tetraploid; most ones contained the complete genomes of both partners in their nuclei, but hypotetraploid plants had lost *pnt* genome parts during regeneration process (Menke et al. 1996). Results of a combination with 50 clones and its partners are given in table 33.

Table 33 Average of 2-4 years of a symmetric (7259) fusion of diploid *S. pinnatisectum* (*pnt*) with dihaploid *S. tuberosum* ssp. *tuberosum* (B15).

Statistic parameter	Foliage blight resistant	Tuber blight resistant	Maturity	Haulmmass	Intensity of flowering	Yield (g/plant	Tuber impression	Tuber size	Tuber defects	Colour of tuber flesh	Starch content (%)
	Clones from fusion										
x_F	3.9	5.7	1.7	5.4	6.2	352	3.3	3.7	3.0	3.7	15.6
s	0.5	0.7	0.4	1.0	1.1	214	0.6	1.0	0.6	0.8	1.2
n	50	50	50	50	50	50	50	50	50	50	50
Max.	5.3	7.3	3.0	7.5	8.0	1007	5.0	5.5	4.0	4.0	17.9
Min.	3.2	3.4	1.4	2.5	3.5	285	2.5	2.5	2.0	2.0	12.7
	Partners of fusion										
pnt	6.3	7.7	1.3	2.2	5.0	28	2.5	2.0	3.0	1.0	26.4
tbr	2.4	4.3	3.5	3.5	3.0	362	5.5	3.5	6.0	6.0	15.3
x_P	4.4	6.0	2.4	2.9	4.0	195	4.0	2.8	4.5	3.5	20.8

The products of fusion with *S. pinnatisectum* showed an insufficient level of foliage blight resistance. A maximal value of 5.3 in the scale 1-9 justified not its use as source of resistance (Table 33). Too low level of resistance was also obtained in fusions of a clone from GLKS 66.71.6.6 by Thieme at al. (1997). Partly similar results mentioned Li et al. (2007). Crossing of *blb* with *pnt* was successfully, but going on with *tbr* is similarly difficult as with its parents (fig. 89).

Other potential sources of resistance used by fusion in Tuebingen were *S. circaeifolium* BGRC 27034 (Oberwalder et al. 2000), *S. okadae* BGRC 028969 and BGRC 028970, and *S. berthaultii*. Examples are given in pedigrees 6.

Pedigrees 6:

1. *oka* BGRC 028969 + GL-VI-87.089.32 diha (1 *dms* 1.56%, *adg*)
↓ x Panda (*dms* 3.12%, *adg*, *vrn*)
↓ Selfing
BAZ-GL-00.1228.01 P Ro1, 2, 3 (1 *oka* 25%, 1-2 *dms* 1.95%, *adg*, *vrn*)

2. *crc* BGRC 27034 + GL-VI-86.109.10 diha (1 *dms* 1.17%, *adg*)
↓ x Rebecca (2-3 *dms* 5.66%, *adg*, *cmm*, *mag)*
BAZ-GL-01.1336.01 P (Sp) Ro 1, 2, 3, 5 (1 *crc* 25%, 2-3 *dms* 3.13%, *adg*, *cmm*, *mag*)

Results of foliage and tuber blight resistance at ZL Gross Luesewitz are shown in table 34 for single clones out of 237 tested in 1998 and 1999 in the field, on detached leaflets, and on tuber slices.

Table 34 Quantitative late blight resistance of 14 clones out of 237 descended from different protoplast fusions, and partly its backcrosses and two fusion partners. Wild species: *S. bulbocastanum* (*blb*), *S. circaeifolium* (*crc*), *S. okadae* (*oka*).

Clone number		Foliage blight resistance				Tuber blight resistance	
		field test		leaf test			
BAZ-GL-Tueb-	Descent	1998	1999	1998	1999	1998	1999
97.03.05	BAZ-GL-87.089.32 + *oka*	8.8	1.0	7.7	9.0	7.7	-
97.08.02	B15 + *crc* BGRC27034	8.7	8.6	8.8	9.0	5.5	5.7
97.10.01	GL5 + *blb* asy	8.6	7.0	8.4	9.0	7.6	-
97.12.04	Pamir + *blb* asy	8.8	7.3	8.1	8.9	5.1	3.5
97.13.02	Regina + *blb* asy	8.7	8.9	8.6	8.5	7.6	-
97.18.02	GL9 + *crc* asy	8.6	8.0	8.5	8.6	5.7	5.9
97.18.04	GL9 + *crc* asy	8.7	7.9	8.4	8.8	7.2	6.7
C4	Irmgard x (B15 + *crc* 109)	8.9	8.6	8.6	9.0	6.0	6.0
C5	Irmgard x (B15 + *crc* 109)	8.9	8.6	8.4	9.0	5.8	7.0
97.25.02	(Irmgard x (B15 + *crc* 109)) x Irmgard	9.0	8.5	8.5	8.8	8.2	8.0
97.26.02	(Irmgard x (B15 + *crc* 109)) x Irmgard	8.7	8.6	8.6	8.9	5.8	2.0
97.27.06	(Irmgard x (B15 + *crc* 109)) x Irmgard	8.7	8.6	8.6	8.9	6.9	6.7
97.31.04	(Irmgard x (B15 + *crc* 109)) x Pamir	9.0	8.2	8.9	8.9	7.3	7.7
97.31.07	(Irmgard x (B15 + *crc* 109)) x Pamir	8.6	7.7	6.6	8.0	7.2	6.7
Irmgard	-	2.6	4.1	3.0	4.2	4.6	4.3
B15	-	4.2	5.2	1.2	4.1	4.0	3.8

Descent (GL9 + *crc* asy) means the asymmetric fusion of a dihaploid *tbr* with a diploid clone from *S. circaeifolium* (*crc*) BGRC 27034, which was treated with X-rays (Oberwalder et al. 2000). Clones BAZ-GL-Tueb-97.08.02, BAZ-GL-Tueb-97.12.04, and BAZ-GL-Tueb-97.26.02 showed a level of tuber blight resistance, which is too low. Irmgard was used two times as backcross parent after minimal assessing blight resistance because of methodical aspects of biotechnology. Breeding points of view did not play an important part at that moment. Results of two years of assessment of resistance correspond well; foliage blight resistance in field assessment correlated with r = 0.64 (B = 40 %), in detached leaf-test with r = 0.93, B = 87%. Clone BAZ-GL-Tueb-97.03.05 (table 34) is an exception because of PVY infection in 1999. Very high scores in test of leaflets (>8.3) of second backcross-clones of *crc* may be caused by an unknown R-gene, which was confirmed by results of a related population with 210 clones showing wide variation of quantitative foliage blight resistance and maturity besides protection by hypersensitivity in a part (fig. 90). Both years tuber blight resistance correlated with r = 0.78 and B = 60 %.

An early late blight resistant clone, BAZ-GL-00.1218.01 P Sp Kr1 Ro1 as a BC3 from *S. crc* was selected in field assessment on foliage (fig. 91). Additionally good tuber form (fig. 92) and suitability for table potato are expressed as well as resistance to *Synchytrium endobioticum* type 1, to *Globodera rostochiensis* Ro1, however, tuber blight resistance is insufficiently.

Last years broadening of genetic basis is carried out using *S. cardiophyllum* (Thieme et al. 2010), *S. michoacanum* (Smyda et al. 2011) and *S. tarnii* (Thieme et al. 2011a). Most of the B2-clones had only 5-7 chromosomes from *S. tarnii* (*trn*), some selected ones had 2-5. Somatic hybrids of *trn* showed compatibility of mitochondrial and chloroplast genomes of both fusion partners, *trn* and *tbr* (Thieme et al. 2011a).

A serious problem in using of selected new sources of resistance for late blight was its partly loss due to high susceptibility to PVY or PLRV (Darsow 2008), not only in this material (Darsow & Hinze 1991a, Darsow et al. 1993, Darsow 2000c) and not only in our pre-breeding (Rudorf 1950, Rudorf & Schaper 1951, Mueller 1951, Kameraz 1964). Wild material and its progeny of cross with *tbr* (F1) were largely virus-infected after two or three years as well in simple greenhouses as in the field, often up to 100%. Crossing was then renounced to reduce spread of virus or was very ineffective because of retarded growth and flowering. Highly virus-resistant cultivated partners for first cross or fusion increase the output and in general the chance of successful use of most potential sources of blight resistance (see pedigree 2.1.). In CIP late blight resistance was intended to combine with resistance to PVY and PVX for use across all potato growing agro-ecological zones and seed programmes (Huaman & Schmiediche 1999). Therefore Thieme tried to select sources of blight resistance with extreme PVY resistance (Thieme et al. 2008, 2010).

In general has to be mentioned that exchange and introduction of any wild or cultivated potato material has to consider the risk of introducing exotic diseases or pests, which requires repeated special tests before growing.

6. Course of breeding, routine of selection, and solution of main problems in pre-breeding for quantitative resistance to *P.* at ZL Gross Luesewitz

6.1. Strategy

Breeding for resistance means breeding for processing, starch or table potato combined with increased resistance. However, using quantitative late blight resistance in variety breeding is more than considering two additional traits (on foliage and tubers) and requires a pre-breeding which considers all important traits of potato from its beginning. Therefore research in a very small group may not be suitable to contribute to practical success. Depending from the type of resistance the procedure from search of resistance donor to combine quality aspects with resistance includes different numbers of cross steps with an increasing interval of 3-10 years for selection of best cross parents and finally release of a variety. At the simplest case of single or combined R-genes (pathotype-specific hypersensitivity) at least 25 years were necessary, if undetected donors were by chance among BC2-3 of available breeding stock (Lehmann 1938a, b, Rudorf & Schaper 1951, van der Plank 1963). Otherwise search of new sources with the new pathotype of *P. infestans* and following cross succession requires more than 30 years to a new variety (see table 1).

Utilization of quantitative resistance is much more difficult than breeding on basis of hypersensitivity because of principal differences of inheritance of both types, which requires lesser strong selection for other traits in using quantitative resistance. A methodical problem is to be sure that late blight resistance of used cross parents is of quantitative nature. Following strategies try to solve the problem:

1. Breeding without R-genes makes assessment of resistance independently from used isolate or races of *P. infestans*. For that cross parents without R-genes have to be bred and selected which includes assessment of the whole material for known R-genes. On this way assessment of resistance in next generations is simplified. There is little doubt that results can be interpreted as quantitative (Turkensteen 1993). Unknown R-genes may be a risk too. Forbes and Landeo (2006) referred to additional unexpected results caused by presence or absence of modifier genes of R-genes (El-Kharbotly et al.

1996). Unintentional selection of clones with a weaker allele of an R-gene is possible in case of a lesser effective multiple allele. This strategy is applied in population B in CIP combined partly with population breeding (Landeo 2002).

2. Utilization of genes for quantitative resistance without excluding of R-genes requires availability and use of pathotypes in assessment of resistance, which overcome all R-genes present in tested material by compatible host/pathogen interaction. The problem is to ensure that the inoculum is pathogen to the whole material tested. Two ways are common:

- 2.1. Assessment of foliage resistance is conducted at a location with naturally extremely high variability of virulence of the pathogen population, for instance at Toluca valley, Mexico. It is assumed that the part of matching pathogens for the whole material is quantitative similarly from the beginning of incidence of the plants. However, outside of centres of diversity of the pathogen this precondition is not fulfilled; that means in nearly all assessment fields for foliage blight resistance with natural infection determined R-genes reduce a part of pathogenic spores and falsify the result in this manner.

- 2.2. Screening with inoculation using the highest possible complex pathotype with high aggressiveness is another way to select for quantitative resistance without elimination of R-genes. Assessment with more than one isolate with highest virulence and quantitative pathogenicity increases the chance to consider the topical parasitic fitness (Latin et al. 1981). Only when results of a potato population follow nearly a random distribution one can assume that disturbing R-genes were not effectively. Clones with the highest level of resistance are repeatedly to assess; testing of its progeny will give certainty concerning the type of resistance. Specially, in case of wild donors of resistance sometimes only the distribution of second cross generation (BC1) enables to conclude to the type of resistance. Highly resistant wild potato clones as from *S. bulbocastanum* tested with known pathotypes of *P. infestans* frequently do not allow the conclusion to the type of resistance, because new R-genes may not be characterised without the adapted pathotype; its absence is probably a question of time and of population dynamics in the field or natural habitat.

Population breeding is considered as most adequate breeding method for quantitative resistance with polygenes (Simmonds 1966, Robinson 1976, Wolfe 1993). Some experiments are known (Simmonds 1969, Plaisted 1983, Glendinning 1989, Haynes & Christ 2006); however, it is not applied in cultivar breeding. For clonal potato breeding from this point of view intercrossing and use of wide-crossing of not related partners and combining of different components of resistance are prior advices. Important is that in succession of crosses up to the new variety on each step the optimal change of the whole complex of traits is achieved. Improving of trait combinations by crossing of resistant wild genotypes with each other or selfing or interspecific crossing at the beginning may reduce later necessary backcross steps. Selection of very different pre-breeding material requires retaining of very different levels of performance as cross parents depending from breeding stage, ploidy level, and inheritance of most to improve traits and maturity. With a minimum of backcross steps the new more resistant cultivar has to be reached, and an important part of breeding progress has to happen in crosses resistant x resistant (intercross). Nevertheless, the obtainable level of resistance is not to improve to its maximum without to be detrimental to fitness of the host (Robinson 1973).

Selection of cross combinations according to the general combining ability from progeny test under greenhouse conditions is recommended to replace phenotypic selection of cross parents (Bradshaw & Mackay 1994). That way generation cycle time in pre-breeding for few selected traits can be drastically reduced. Crosses with best GCA for late blight are repeated and common selection is then carried out at SCRI. However, concentrated attention on some traits improvement can only be meaningful as additional measure, not for the normal breeding programme. This strategy maybe suitable for material on cultivar level only because of low drawbacks in traits not selected for. In our pre-breeding with more wild material this suggestion has not been accepted. The complex polygenic determined traits can be selected on phenotype, but better by using the offspring-midparent regressions for choice of cross parents.

Genetic diversity of used late blight resistance is intended in our strategy of breeding to strug-

gle against adaptation of the pathogen on variety level in future. That requires permanent broadening the basis and reduces the input in progressed pre-breeding material because of limited manpower. One has to find the right balance between introduction of new sources and development of progressed breeding stages by inter-crossing and backcrossing.

6.2. Course of breeding in pre-breeding

The course of breeding describes the succession of cross generations, mainly as pair crosses. In retrospective view it is given by the descent of a clone and in preview by the planned cross order. In present, the decision, which parents are crossed with each other and why these and not other, make a crucial point of breeding success. More than in cultivar breeding planning of sequence of crosses over several generations in advance is important in pre-breeding because of huge differentiation in expression of traits due to use of wild cross parents. Often only polygenes for late blight resistance are of interest in the donor clone; the result of first cross with *tbr* is a dramatic back-stroke in nearly all other traits. For instance plants grow very slowly and flower up to frost finishes vegetation; a high part of the progeny develops no tubers or very little ones (see fig. 72) with deep eyes and very bad taste; stolones are often more than one meter long and come up as new stem; physiological disorders on tubers may be a problem and susceptibility to scab, *Alternaria* sp. and virus diseases can be higher than in cultivars. Male fertility usually is absent. In all traits pre-breeding has to change the 'wild' stage to a cultivar-near level as it is shown in figure 72 for tuber shape and tuber size. Already for monogenic dominant inherited R-gene resistance to late blight this breeding task was described as difficult (Schmidt 1933). However, using a polygenic determined trait from wild species is much more difficult; one has to take counter-measures against distribution of desired alleles in meiosis, which result in reduced possibilities for selection of other traits.

D-, E- and F-clones are grown the sixth to eight year after sowing for final assessment of traits and final selection (D-clones) and for crossing. About three different cross parents are picked out for each parental clone individually. For resistant E-clones only usable as seed parent the choice of suitable pollen parents is more delimited than for male fertile ones. Clones of wild species are crossed with cultivars (breeding course 1, 2 or 4 in table 35) or wild clones (breeding way 3 in table 35). For diploid clones best male or female fertile dihaploids of *tbr* or a wild clone are preferred to tetraploids, because overall-breeding progress on diploid level with our diploid material is very hopefully. Expression of quality traits of a blight-resistant wild clone or its BC1 determines the utilization in future for starch, table potato or processing. These long-term aim of combination breeding, for instance development of highly blight-resistant material for processing, will be subdivided into aims for each cross up to expected new cultivar. Experience and talent of a breeder are mainly effectively in that, to reduce a progeny in the right measure depending from the breeding stage (F1, BC1 …), and not to expect more from a cross than the parents put in. With the best clones of the best combinations one has patiently to go on. Priority of the traits changes from breeding stage to breeding stage. Polygenic inherited traits take highest attention from the beginning and during the whole course. A pre-breeder has more than a variety breeder flexible to adapt the selection limit to each progeny depending from breeding stage and parent's value with different expectation.

The following sequences of crosses of wild species (W) with cultivated potatoes (*tbr*) were applied (following the arrow) in our pre-breeding practice (table 35). Cross of species (F1) and single backcross stages (BC1-BC5) are explained in first breeding way. Usually the female cross partner (seed parent) is written first and the male one (pollen parent) on second position, here both is exchangeable.

Table 35 Breeding courses in pre-breeding to transfer quantitative resistance from wild species into cultivated potato genome at ILK.
W = clone of wild species, *tbr* = *S. tuberosum* ssp. *tuberosum*, F1 = progeny, BC = backcross

Course 1: poor backcrossing
W x *tbr* = **F1**
(W x *tbr*) x *tbr* = **BC1**
((W x *tbr*) x *tbr*) x *tbr* = **BC2**
(((W x *tbr*) x *tbr*) x *tbr*) x *tbr* = **BC3**
((((W x *tbr*) x *tbr*) x *tbr*) x *tbr*) x *tbr* = **BC4**
(((((W x *tbr*) x *tbr*) x *tbr*) x *tbr*) x *tbr*) x *tbr* = **BC5**;

Course 2: backcrossing and inter-crossing
W x *tbr*
(W x *tbr*) x *tbr*
((W x *tbr*) x *tbr*) x *tbr* = BC2
BC2 x BC4
(BC2 x BC4) x *tbr*
((BC2 x BC4) x *tbr*) x BC5
(((BC2 x BC4) x *tbr*) x BC5) x *tbr*

Course 3: crossing within or between wild species followed by backcrossing and inter-crossing
W x W = F1a
(W x W) x *tbr* = F1b
((W x W) x *tbr*) x *tbr* = BC1
((W x W) x *tbr*) x *tbr*) x *tbr* = BC2
BC2 x BC2
BC2 x BC2) x *tbr*
((BC2 x BC2) x *tbr*) x BC5
(((BC2 x BC2) x *tbr*) x BC5) x tbr
[(((BC2 x BC2) x *tbr*) x BC5) x tbr] x [(((BC2 x BC4) x *tbr*) x BC5) x tbr]

Course 4: backcrossing and inter-crossing
W x *tbr*
(W x *tbr*) x *tbr*
((W x *tbr*) x *tbr*) x BC4
(((W x *tbr*) x *tbr*) x BC4) x *tbr*
((((W x *tbr*) x *tbr*) x BC4) x *tbr*) x BC4
(((((W x *tbr*) x *tbr*) x BC4) x *tbr*) x BC4) x *tbr*
((((((W x *tbr*) x *tbr*) x BC4) x *tbr*) x BC4) x *tbr*) x BC5

Breeding course 1 corresponds with classical backcrossing and is the appropriate method for simple inherited and dominant expressed resistance as potato canker or race-specific blight resistance (R-genes). It took 3-7 backcrosses to transfer a major dominant resistance gene from a wild species into a successful cultivar (Reddick 1943, Black 1947, Schick & Schick 1961, Ross, 1986, Bradshaw & Ramsay 2005). Bos (1980) recommended at least six backcrosses for elimination of undesired 'wild' alleles. Saving of one to two backcross generations are expected to be possible for quantitative late blight resistance from wild species by combining conventional breeding and selection with molecular markers (Trognitz et al. 1996). Using marker-assisted selection with three backcross steps 99% of the cultivated genome can be recovered, instead of 6-7 generations required for the same level conventionally (Barone 2004). That seems imaginable only for positive selection of one or few monogenic dominant trait(s) and ignores absence of markers for the majority of other traits to reduce the linkage drag (Gebhardt et al. 2006), particularly for quantitative traits. However, even in a simple case Tan et al. (2005) stated in breeding material poor diagnostic potential of used marker loci for qualitative nematode or late blight resistance. In case of late blight resistance determined by polygenes, probably more than 10-15 genes have to be identified and maintained.

Also for MAS much more genetic knowledge is necessary and more available markers are required before changing from conventional to molecular selection could be decided in breeding practice. In opposite to common scientific proposals is to consider that pre-breeding for quantitative resistance has many other target traits from the beginning; it is not in the focus of MAS up till now and next future to assist combining of polygenes for yield, maturity, quality com-

plexes and resistance at the same time starting with interspecific crosses (see results of Sliwka et al. 2005, only for quantitative late blight resistance). Here much more research is necessary.

The part of progeny with foliage blight resistance score ≥7 often falls from about 95% in *S. demissum* to nearly 90% in F1, 15-20% in BC3 und <10% in BC4 in series of backcrosses. Loss of genes for resistance is supported by down-regulation from pentaploid F1 to the tetraploid level and distribution in the progeny. Rivera-Pena (1992) determined 28% resistant seedlings in BC1; Kirsanova et al. (1989) found about 6% useful recombinants in BC3. If tuber blight resistance is desired at the same time, only 1-2% remains in course of selection in BC4 due to blight resistance (Darsow 2000b). The used backcross parents influence the part of resistant clones in the progeny. It is impossible to select for all the other traits among 2% of the progeny.

Therefore pure backcross is unsuitable for polygenic resistance – a multiple experience, rarely published (Tazelaar 1981). Ross (1986) mentioned that the *dms*-introductions to most of the cultivars today had hardly any effect on its blight resistance. Dispersion of resistance alleles among the progeny and selection for many traits against its 'wild' expression do not realize high midparent-offspring correlation in breeding practice in opposite to Stewart et al. (1994) in research. It is badly that the common opinion on value of polygenic resistance is based on unsuitable breeding practice (as in case of Allefs et al. 2005) and that the hint of Toxopeus (1964) to apply backcrossing as rarely as necessary has been disregarded.

Already Niederhauser (1962) explained his strategy to combine many sources of multigenic resistance in promising selections. This is continued in Mexican breeding, in which a mix of horizontal resistance with R-genes is applied and both parts are not discriminated (Rivera-Pena 1992). Sidorov (1937) named such system accumulating breeding. Parlevliet (1993) recommended recombining of resistant clones which should be genetical diverse (Buddenhagen 1981). Simakov et al. (2008) accumulated polygenes for quantitative foliage blight resistance by 2-3 saturation crosses and selection of transgressive segregates. Because potential for quantitative resistance exists in susceptible potato clones too (Umaerus & Umaerus 1994), always both parents influence the resistance level of the progeny. Above mentioned breeding courses 2-4 consider these recommendations. The breeding course to nearly the same backcross step requires 1-3 cross steps more which takes 8-24 additional years (table 35). In this manner distribution of alleles for resistance in backcrossing has to be compensated by introduction of new or additional ones. In advance to the main cross succession one has to breed necessary best suitable cross parents as programme in parallel (Schnell 1983), because otherwise they are not available.

Table 36 Breeding course to produce *Phytophthora*-resistant cross parents at ZL and levels of four traits according to our experience. Score 9 = highest possible positive expression (very early, highest resistance or quality). Last line: expected level realized in variety breeding according to our scale.

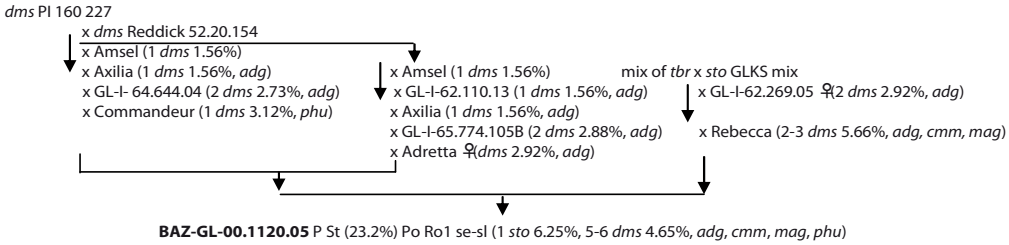
	Phytophthora-resistance			
Parents/cross steps	Foliage	Tubers	Maturity	Table quality
Wild species	9	9	1	1
Variety	2-3	3	6	8
Wild species x variety	9-7	9-7	1-2	1-2
Backcross 1 (BC1)	8-6	8-6	1.5-2.5	2-3
Backcross 2 (BC2)	6.5-5	7-5	2-3.2	2.5-3.5
BC2 x BC4 = BC2.8	8-5	8-5	2.3-4	2-3.7
BC2.8 x variety = BC3.8	6.5-4	6-4	2.5-4.5	3-4.5
BC3.8 x BC4.5 = BC4	8-5	8-5	2.7-5	2-4
Backcross 5 (BC5)	6.6-3.5	6.5-3	3-6	3.5-5.8
BC5 x BC4 (handed over)	7.7-4.5	7.5-4.5	3.3-6	3.8-5.3
New variety after 2 additional crosses	6.5-5	6.5-5	3.5-7	5-6.5

According to the experience in our institute crosses resistant x resistant in mix with backcrossing are essential to remain a good level of resistance (table 36). Back-crossing introduces necessary variability for cultural traits and causes partly loss of resistance. Inter-crossing resistant x resistant accumulates resistance alleles (to prefer from different sources) and should combine desired alleles for other traits at the same time. Some preconditions have to be fulfilled for that: a genetic broadly based pre-breeding material, diverse resistant pollinators, strongly reduced susceptibility to virus diseases, breeding garden located in a region with low aphid population density. Of course, the given examples 2-4 of the breeding course may be varied. BC2 x BC4 results in BC2.8, BC2.8 x *tbr* leads to BC3.8; progeny of BC3.8 x BC4.5 results in BC4 by chance (Darsow 1998a). Additionally selfings are used.

The expected scores for new varieties correspond to our assessment conditions, in which score 6 means a higher level than 8 (or 2 in German list) in common variety lists.

Pedigree 7 gives an example for intercrossing with improvement of blight resistance and other traits at the same time. BAZ-GL-00.1120.05 is a very highly blight resistant BC3 from *sto* and BC3.6 from *dms*, is suitable for starch (St) with a content of 23% in average of four years and suitable for French fries (Po), resistant to Ro1 and second early to second late. Genes of four additional species may be present.

Pedigree 7:



In spite of mentioned contrast of quantitative blight resistance to R-gene resistance there were similarities on breeding level in the last stage of using hypersensitivity and in breeding for quantitative resistance in so far as

1. crosses resistant x resistant were necessary to combine different R-genes (Reddick & Peterson 1947);

2. the outcome of complex resistant progeny was partly very low depending from the number of involved genes and required much higher numbers of seedlings than at the beginning of R-gene breeding (Schick 1932, Schick & Lehmann 1936, Rudorf & Schaper 1951, Kameraz 1968);

3. complex interspecific hybrids were bred too because of hope for including higher genetic diversity of resistance than detectable at the moment. It was learned that after successful combining go on by backcrossing is disadvantageously (Rudorf & Schaper 1951). The practice of Withworth et al. (2007) with foliage assessment in the field and laboratory including single hill assessment at Toluca, and field test for late blight resistance seems to use a mixed model for qualitative and quantitative late blight resistance. Schmiediche (1987) considered 7-8 cross steps to be necessary from the wild species to new cultivar.

4. priority of selection for late blight was requested by Rudorf (1950) because assessment in later selection stage can identify only a small part of originally existing individuals with desired combination of resistance genes.

Pre-breeding of quantitative blight-resistant clones requires 6-8 cycles of cross and following selection, which takes 3-4 years at the beginning with wild species, in F1 6 years, from BC1 on 6-8 years. In best case, a change of tuber shape and tuber size succeeds as in figure 72. Similarly other traits should be expressed on a cultivar-near level, combined with high blight-resistance on foliage and tubers to be handed over to cultivar breeders. They produce new cultivars with a better level of resistance than present by one or two additional cross steps. The given scores are not comparable to that given in variety lists because of stricter assessment in pre-breeding. Altogether, 7-10 cycles has to be assumed to transfer quantitative late blight resistance from wild species to a successful cultivar for conditions of Middle Europe. This is a real expectation which requires stable long-term planning and high qualified execution. Molecular-marker assisted introgression of wild genome will offer the possibility of faster progress up to BC2 than can be achieved by traditionally backcrossing. Later on molecular-marker assisted selection has to consider polygenes for late blight resistance.

For each potential cross parent with high resistance to *P. infestans* its utilisation is to decide, better in breeding stage BC1 than in BC2, because the wild, highly resistant clones frequently have a poor level of quality traits. Subprogrammes for starch, table potato and processing reduce production of resistant clones without qualitative purpose. Since quality traits are determined mainly by oligo- or polygenes, the combination with quantitative resistance requires combination-(or accumulation-)breeding for quality aspects too. That means resistant clones with low quality (if the combination in the source of resistance is absent) are to use by crossing in one subprogramme for stepwise combining quality and resistance. Therefore, a number of blight-resistant, unrelated and male-fertile cross partners are necessary. For instance, in sub-programme for French fries is intended at the same time to combine two resistant parents which complement each other by different components of foliage blight resistance (resistant to infection, resistant to spread, low spore production) in following intercross: parent 1 (suitable for French fry by low discolouration, good foliage and tuber resistance) x parent 2 (suitable for French fry by large and long tubers, middle discolouration, good-middle foliage and tuber blight resistance). A mix of backcross and intercross enables to breed the parents needed to go on to the true aim.

In table 37 is shown which part of new cross parents could be selected from different cross types of our pre-breeding material sown in 1995 and 1996.

Table 37 Result of selection in pre-breeding material for resistance to *P. infestans* sown in 1995 and 1996 at ZL Gross Luesewitz (Darsow 2002b).

			Number of seedlings with				
Year	Type of cross concerning blight resistance	Number of cross combinations	*P. infestans* inoculation	foliage blight resistance	good tuber shape	resistant tubers	Number of selected new cross parents
1995	Resistant x susceptible	21	7896	2648	596	319	0
	Resistant x resistant	55	11987	5930	816	582	14
	Selfing of resistant	27	8162	4605	1190	803	3
1996	Resistant x susceptible	22	8099	2603	842	564	4
	Resistant x resistant	17	4939	2023	671	426	10
	Selfing of resistant	4	1915	295	191	143	1
	BC1-BC3 of new sources	46	9848	5515	757	667	19
	BC4, dihaploid production	16	456	-	281	193	6

No one new cross parent could be selected out of 21 backcross combinations with 376 potted seedlings in average per cross after selection for foliage blight resistance from sowing year 1995 (first line in table 37). In material from 1996 after six years selection at the same group four new cross parents were picked out. Compared to it, from crosses resistant x resistant an evident higher part of cross parents was selected. Selfings assist selection of resistant individuals in case of recessive inheritance (Friedt & Ordon, 1995), but our results do not indicate on importance of that (table 37, 38). However, pollination of tetraploid BC4 of *S. demissum* with *S. phureja* (*phu*) resulted besides dihaploid and triploid progeny some tetraploid descendants with changed genome, which itself outstanding frequently recommended as new cross parents as unintentional by-product of dihaploid production. DNA rearrangement in dihaploid production is observed by Ercolano et al. (2002).

From the data of table 37 was calculated, how many seedlings in each group were necessary to find one descendent as new cross parent to produce next generation (table 38). In case of crosses of resistant BC4-5 x susceptible parent nearly 4000 seedlings were required in opposite to BC1-BC2 x susceptible parent with about 500 and selfings with 2500. Crosses resistant x resistant demand 700 seedlings to select one clone as parent for next generation. On diploid level calculated number is too small because of gingerly throw away. The analysis within the successful cross combinations showed smaller differences, which is interpreted as effect of better combining ability.

Table 38 Number of cultivated seedlings in pre-breeding for resistance to *P. infestans* necessary to find one new cross parent in material sown 1995 and 1996.

	Necessary number of seedlings to select one new cross parent	
Cross combination	from all crosses	from crosses in which new parents were selected
BC4-5 x susceptible cultivar	3899	356
Selfing of BC4-5	2519	563
BC4 x BC4-5	705	316
(F1, BC1, BC2) x susceptible variety	518	170
Production of dihaploids	91	43

This analysis shows that specific breeding strategy, a long-term concept and more than a small group of persons involved are necessary to combine quantitative late blight resistance with

other traits on nearly variety level. Salaman (1931) found in certain cross populations of poorly domestic parentage only about one resistant seedling in 300 ones.

6.3. Routine of selection and considered traits in pre-breeding for resistance to *P. infestans*

The scheme of selection describes the procedure of evaluation of traits and the reduction of the material from about 400-600 individuals per population as seedlings to 0-3 potential new cross parents seven years later to produce the next potato generation. In variety breeding find out of a new cultivar is intended additionally. The system of selection describes succession and intensity of elimination of genotypes according to their expression of traits in different years and conditions. Selection begins sometimes before sowing of the seeds, generally after emergence and continues. Selection can be systematized according to age of plants. Plants of first year are seedlings, of second year single hills in the field. Only in case of wild material or sometimes BC1 cultivation in greenhouse is preferred. The third year of a clone is usual the second year of growing in the field, such clones are named A-clones. Each next year takes the next letter of alphabet. D-clones are six years old and in pre-breeding that is common the last year of intensive evaluation. Evaluated traits are listed in table 39 from first to sixth year in chronological order.

Table 39 Scheme of evaluation and selection in pre-breeding for quantitative blight-resistance at ILK Gross Luesewitz.

Year	Term of clones	Examined traits
1	Seedling	Foliage blight resistance, growth habit, stolon length, tuber size, tuber shape, eye depth, tuber deformation, tuber blight resistance.
2	Single hills	Virus diseases, intensity of flowering, stolon length, tuber size, tuber shape, beauty of tubers, eye depth, internal tuber defects, scab, tuber deformation, cracking, soft rot, tuber blight resistance, dormancy.
3	A-clone	Uniformity of emergence, juvenile haulm growing, haulm mass, recognizability of virus diseases, intensity of flowering, colour of flower, set of berries, growth habit, attack with *Alternaria* sp., stability of haulm, plant height, maturity, stolon length, yield, general impression of tubers, tuber size, beauty of tubers, uniformity of tubers, imperfection of tubers, tuber shape longitudinal and crossways, eye depth, hilum, scab, soft rot, dry rot, black scurf, tuber deformation by *Rhizoctonia solani*, skin colour, roughness of skin, cracking, internal rust spot, hollow heart, flesh colour, starch content, tuber blight resistance, suitability for crisps, resistance to nematode Ro1, Pa2, Pa3.
4	B-clone	Uniformity of emergence, juvenile haulm growing, haulm mass, recognizability of virus diseases, intensity of flowering, colour of flower, set of berries, growth habit, attack with *Alternaria* sp., stability of haulm, plant height, maturity, number of stems per plant, % of plants with stunting and rosetted top by *Rhizoctonia solani*, stolon length, yield, general impression of tubers, tuber size, beauty of tubers, uniformity of tubers, imperfection of tubers, tuber shape longitudinal and crossways, eye depth, hilum, scab, soft rot, dry rot, black scurf, tuber deformation by *Rhizoctonia solani*, skin colour, roughness of skin, cracking, internal rust spot, hollow heart, flesh colour, starch content, number of tubers per plant, tuber weight average, suitability for crisps, suitability for French fries, duration of dormancy, discolouration of raw tuber flesh, blue bruise, discolouration after cooking, appearance after cooking, consistency after cooking, disintegration during cooking, mealiness, taste, cooking type, index of culinary quality, resistance to nematode Ro2, Ro3, Pa2, Pa3, attack with viruses PVY, PLRV, PVM, PVS, PVA, PVX, tuber blight resistance in slice test and in whole tuber-test, foliage blight resistance in single leave test and in field assessment.
5	C-clone	The same traits are evaluated again. Additional assessment of nematode resistance to Ro 5, to PVY, PLRV, PVM, PVS, PVA, PVX, PVS, to soft rot, to dry rot, to potato wart disease pathotyp 1, draught tolerance.
6	D-clone	The same traits are evaluated again. Among nematode resistance only that to Pa2, Pa3 is repeated. Clones with resistance to potato wart disease pathotype 1 are tested to pathotype 18. Male and female fertility are tested.

Table 39 records 79 traits, which are considered. Not for all breeding material the whole programme of evaluation of traits can be applied, for instance on wild material. Selection of sourc-

es of blight resistance begins with three-year assessment of resistance of foliage and tubers and selection of a few other traits as virus infections, stolon length, tuber shape, tuber size, eye depth, tuber deformation, male and female fertility (fig. 77, 78, 81) and leads to choice of single wild clones for crossing with *S. tuberosum*. After sowing its progeny as F1 (fig. 93) more traits are possible to examine, because of better tuberization. Selection follows mainly table 39. Who one times has seen wild potato plants or its progeny from crossing with *S. tuberosum* ssp. *tuberosum* at harvest in the field has an impression of the task of pre-breeding. The expression of traits is very far from that in cultivar breeding material (Schick 1932, Schmidt 1933, fig. 54). Therefore the scales for evaluation applied in pre-breeding are wider than that for cultivar breeding. Often not before BC1 (see table 36) tubers of sufficient number and size can be produced for the whole programme of table 39. In case of quantitative traits decision for elimination of clones according to results only of the present season (only one year considering) occurs, if very negative expression is obtained. Otherwise, two or three year's average is the basis of decision in selection.

Appropriate conditions in greenhouses and on field enable best expression of genetic potential. However, the following results of 69 clones from fusion of *S. bulbocastanum* (*blb*) with *S. tuberosum* (*tbr*) show that some traits should not be selected on greenhouse grown plants (table 40). The material was cultivated two years each in parallel in greenhouse and in the field. Expression of 10 traits was estimated.

Table 40 Correlation (r) of traits in greenhouse (GH) and field, two years average of 69 clones of fusion combination 6979, *blb* + *tbr*. (B (%) = r^2x100.).

Trait a	Trait b	r	B (%)
Mass of foliage in GH	Mass of foliage in field	0.780	60.9
Intensity of flowering in GH	Intensity of flowering in field	0.794	63.1
Set of berries in GH	Set of berries in field	0.143	2.0
Yield in GH	Yield in field	0.775	60.0
Tuber size in GH	Tuber size in field	0.760	57.8
Beauty of tubers in GH	Beauty of tubers in field	- 0.050	0.2
Beauty of tubers in GH	Overall impression tubers in field	0.149	2.2
Deformation of foliage field	Deformation of tubers in field	0.513	26.3
Foliage blight resistance	Hairiness of leaves	0.096	0.9
Foliage blight resistance	Tuber blight resistance	- 0.101	10.3

Whilst mass of foliage, intensity of flowering, yield and tuber size correlated similarly in its expression under greenhouse and field conditions, set of berries and beauty of tubers in greenhouse were not representative for its behaviour in the field. These results correspond mainly with comparison of evaluation of *tbr*-clones in greenhouse (seedlings) with following field-grown years (Maris 1966, 1988). Hairiness of leaves played not an important part as factor of foliage resistance as expected because of low variation in very high foliage blight resistance. Tuber blight resistance tested on slices showed no connection to foliage blight resistance, even very near to wild level of resistance. If tuber blight resistance is not tested and selected for, one has to expect loss of main part of responsible genes of resistance of tubers.

How many seedlings are necessary to find a very well potato clone from one or ten seedlings population(s)? A large population size is recommended (Brock 1967, Robinson 1973). Sim-

monds (1969) stated following example for selection: Suppose we retain 10% of genotypes for yield, tuber shape, cracking, cooking quality, blight resistance, resistance to PLRV, and scab resistance, each; 20% of seedlings each for tuber size, foliage type, flesh colour, resistance to gangrene, to skin spot, dry rot and black leg; and 50% each for skin colour, resistance to wart and PVY. The traits are assumed to be genetically independent, so only one in about 10 million individuals (clones) would satisfy all these 17 criteria. The calculation considered only 17 traits. Independence of the traits is not in all cases realised. Moeller and Pfeffer (1965) mentioned that 100 years ago a variety could be selected from about 500 seedlings; however in 1965 the 20 most important traits are expected only sufficiently by retaining one of one million seedlings. Holden (1977) discussed selection for 40 traits in potato breeding. Increasing number of traits being assessed and suitability for export required higher seedlings production from more diverse crosses and longer trailing in more environments (Bradshaw 2009). Iwanaga (1984) mentioned the necessity to work with high seedlings numbers even on diploid level. In CIP yearly 20-30 000 seedlings were selected for late blight resistance, 50,000-100,000 were planned in future (Anonymous 1983). 65,000 seedlings for late blight resistance are mentioned in the report for 1989 (Anonymous 1989). 40,000-55,000 seeds have been sown in ZL Gross Luesewitz from which about 10,000 foliage-resistant seedlings were grown yearly.

An example for quick reduction of individuals by selection of pre-breeding material during six years is given in table 41 according to the long-term average. At the beginning the number of inoculated seedlings is given. The written percentage of eliminated genotypes refers to present individuals in stepwise selection.

Table 41 Selection in pre-breeding for quantitative resistance to *P. infestans* at ZL

		Reasons for throw away and % of eliminated genotypes because of							
		Susceptibility to				Intensity of flowering			
Year	Number of clones present	Foliage blight	Tuber blight	Attack of viruses	Traits on haulm		Traits on tubers	Quality traits	Part (%) of kept seedlings
1	30732	60	33	0	3	0	60	-	10.84
2	3330	-	19	2	0	12	70	-	2.24
3	690	-	21	13	7	4	38	33	0.56
4	171	6	7	10	6	8	28	22	0.17
5	52	13	9	2	2	0	12	18	0.08
6	26	15	16	0	0	0	14	21	0.004

After six years evaluation 11 E-clones remained for crossing, four of these were offered private breeding companies to produce new cultivars with improved blight resistance by crossing with it.

Important is the old principle in selection to preserve the donor genes for resistance (Hermsen 1977), and that means giving selection for resistance priority to other traits. Compared to cultivar breeding a very intense selection during first years is carried out, but it is not intense early-generation visual (positive) selection. It is to consider that using wild potatoes results in a much higher genetic variability of eye depth, length of stolones, maturity, or tuber shape in such progenies up to BC4 in opposite to such of cultivar breeding. Indeed, we apply only negative selection; the danger of wrong decisions is lesser in pre-breeding than for instance, in cross prediction according to 'breeders preference' at the breeding stage for parental line selection by Brown and Dale (1992). For instance in 1995 24,000 seedlings (BC3-BC5) were inoculated, from which 10% got foliage blight resistance score 9, 17% score 8, 28% 7, and 8% 6, the rest (37%)

was discarded. From the 24,000 seedlings 8,700 were potted. Selection for eye depth, length of stolon, tuber shape and tuber size reduced the number to 4200, which decreased to 2,200 by tuber blight resistance test. These were planted in the field as single hills (single spaced plants) with 1 m distance in the following year. Owing to selection for flowering and tuber traits in the field only 725 clones were harvested. Tuber slice test resulted in blight resistance score 9 at 3%, 8 at 25%, 7 at 23%, and 6 at 13%. Repeated observation of the tubers according to table 40 reduced 68% of clones with score 6 in slice test, 34% with score 7, 26% with score 8, and 9% with 9 due to different compromises depending from level of resistance. A-clones of 1995 tested in tuber slice test get 2% score 9, 30% score 8, 31% 7, 28% 6; the B- to D-clones resulted in following groups of tuber blight resistance: 1% score 9, 24% score 8, 35% score 7, 29% score 6. From these four groups following percentage was planted in 1996: 0%, 75%, 65%, 36%. Foliage blight resistance in detached-leaflet test of 168 A-clones of mainly F1 generation from crosses directly with wild species resulted in 39% score 9, 18% score 8, 10% score 7, 4% score 6, and 29% score 5 and lesser. In assessment of whole tubers late blight resistance of this material 76% of the clones had score 7-9.

Our seedlings selection is at the same time carefully used as progeny test. One backcross parent is used as tester; two other cross parents supplement the result with about 200 seedlings each. Best cross combinations are repeated and best inheritors of blight resistance are preferred, but other traits are considered for such decisions and often these played a more important role. In future, genetical knowledge and molecular markers should play its part in selection strategy, but not before its higher effectiveness is evident compared with conventional practice.

In SCRI Dundee since 1985 breeding progress has been tried to accelerate by using progeny test for foliage and tuber blight resistance, resistance to white cyst nematode, yield, tuber appearance, fry colour and its combination to estimate best parent combinations; other whole progenies are discarded. Selection of field-grown material is focussed only on these best combinations from progeny test and its later repeat; increased efficiency saves trail area and expenditure of work. Five cycles of selection in seedlings stage with parent selection in between are carried out in 18 years for quick combining of the mentioned traits in superior cross parents for commercially funded variety breeding (Bradshaw 2009). Quick selection for only few traits does not meet requirements of cultivar breeding according to our understanding. However, breeding for quantitative blight resistance on only seedlings based selection is not acceptable for us.

6.4. Growing system in pre-breeding of ZL and the pre-breeding stock available in 2006

Our system of growing is connected with the scheme of selection. Its main part is carried out on one location, at ZL Gross Luesewitz. Seedlings are grown at greenhouse, exceptionally is a long tradition of negative seedlings selection for foliage blight resistance and assessment of each seedling for tuber blight resistance on tubers grown in pots. One tuber per seedling is grown next year in field (single hill). Subsequently clones are grown in field while interest is given for evaluation, for using as cross parent in pre-breeding, cultivar breeding or production of material for scientific purpose or exhibitions. Only the best 5% of clones (0-10 per year) are cultivated *in vitro*. From stage of B-clone onward growing of each clone is local split into

1. plot for multiplication with reduced vegetation,
2. plot for evaluation of traits (examination of performance), harvest after maturation,
3. plot for field assessment of foliage blight resistance with inoculation (virulence 1-11), protection against wind, irrigation, without fungicides (fig. 94),

4. plot for assessment of tuber blight resistance (whole tubers inoculated on day after harvest),
5. field assessment of resistance to virus diseases at Aschersleben/Quedlinburg with very intensive development of aphid populations without chemical plant protection,
6. plot for crossing,
7. plot for F1 and BC1 of 'wild' material included multiplication and examination separated from 1.-2., because of late maturity and susceptibility to virus diseases.

Since each year new crosses are made and new seeds are sown each year a new selection cycle from seedling to D-clone is started. All stages of selection are present in a given year.

A location as Gross Luesewitz really only enabled efficient working with wild potatoes in pre-breeding, because it is located in the "healthy region for seed potato production in M-WP" and at the same time within the „high grade region", which is officially recognized by EU. These conditions make very low infection pressure from surrounding potato fields (4.6.1.). Several years' growing of segregating populations or of wild cross parents was only here possible, even without seed production from *in vitro* culture.

In 2006 following pre-breeding clone numbers were grown for different objects (table 42).

Table 42 Growing of pre-breeding material of 4.-6. year in the field for different objects at ZL Gross Luesewitz in 2006.

Material	Number of clones	
Seed potato production	181 early to second early	368 second early to second late
Examination of performance	169 early to second early	210 second early to second late
Field assessment of foliage blight	179 early to second early	199 second early to second late
Whole tuber blight resistance	169 early to second early	217 second early to second late
Field assessment of resistance to virus diseases		379 clones
Plots to produce stem cuttings for crossing		271 clones
Wild material (F1, BC1)		18 clones
Field assessment of foliage blight resistance for genetic analysis		2 x 942 clones
Seed potato production of clones for genetic analysis		932 clones

The last two lines in table 42 are connected with an additional project. Intensive evaluation of B- to D-clones was carried out in other years usually in similar extent. In 2006 379 clones were grown in three-years evaluation of diverse traits (fig. 95, fig. 96), 378 for three-years testing of foliage blight resistance (see Fig. 21), and 386 for three-years assessment of tuber blight resistance on whole tubers freshly harvested. In this manner the 79 traits recorded in table 40 are evaluated.

Production of healthy seed potatoes included in 2006 besides the B- to D-clones written in table 42 and 43 additional those which could not be assigned to use for ware potato or starch or processing as well as elder resistant ones and cultivars of interest, altogether 650. High attention is directed to continuously visual observation of symptoms of virus diseases or deviated appearance with early elimination of plants deviated from healthy look. From about middle of July on haulm is killed depending from maturity. Excised-bud assay starts on A-clones with five tubers; up to 20 tubers are grown from elder clones; 10 plants are tested by ELISA in February for virus infections (table 39, table 42). The living collection is remained nearly healthy except for PVS, alone by elimination according of symptoms or results of ELISA, without *in vitro* cultivation.

Field assessment of virus resistance starts with 10 tubers of harvested A-clones from Gross Luesewitz for successive three-years growing at Quedlinburg without selection (see 4.6.1.).

In 2006 were harvested: 0 seedlings, 1890 single hill-clones, 341 A-clones, 234 B-clones, 57 C-clones, 52 D-clones, 220 elder clones and cultivars.

The biggest part of pre-breeding material for blight resistance has sub-programme 'ware potato', followed by 'starch' and 'processing' (table 43). Clones with very high level of combined virus resistance are necessary to overcome the mostly very high virus susceptibility of sources of blight resistance; such cross parents are at hand from long tradition in breeding for virus resistance in past. Resistance to *G. pallida* is intended to combine with blight resistance and high starch content (6.5.4.3.).

Table 43 Number of own tetraploid and dihaploid pre-breeding clones of different utilization in seed potato production 2006.

Utilization	Ploidy	Early to second early	Second early to second late
Resistance to *P. infestans*/ware potato	4x	68	61
Resistance to *P. infestans*/processing	4x	28	21
Resistance to *P. infestans*/starch	4x	24	33
Processing, starch	4x	4	8
Resistance to *Globodera pallida*	4x	9	15
Resistance to virus diseases	4x	8	10
Resistance to *P. infestans*	2x	8	13
Processing, starch, table quality	2x	23	24

6.5. Solution of main problems in pre-breeding for quantitative blight resistance

Following main problems were essential to solve:

1. overcome the very high susceptibility to virus diseases of most sources of blight resistance,
2. combine resistance of foliage and tubers to *P. infestans* (6.5.2.),
3. separate the influence of maturity from true quantitative foliage blight resistance in calculation of resistance from disease progress (4.2.3., 4.2.4., 6.5.3., 7.2.),
4. combine late blight resistance with high level of quality traits (6.5.4., 7.4.-7.6.),
5. combine blight resistance with resistance to *Erwinia* sp., *Fusarium* sp. and insensitiveness to mechanical damage (6.5.7., 7.5.).

Because of the mentioned traits are determined by polygenes or oligogenes, the problems can not be solved successively, but they have to be worked on at the same time. Successful combination of quantitative resistance with good expression of traits of potato utilization in pre-breeding is a precondition that cultivar breeding is willing and able to transfer this type of resistance with moderate to low inheritance to new cultivars. Therefore the author went his own way with a long-term strategy, independently from international trend. Following aspects were essential:

1. Selection of clones of wild species blight resistant on foliage and tubers as sources of resistance, and its selection to other traits as much as possible (chapter 5.1.4., 5.2., 5.4., 5.5.).
2. Realize priority of quantitative resistance to *P. infestans* to other traits in succession of selection (see 4.2., 4.4., 6.2.).
3. To assure compatible host/pathogen interaction by inoculation with isolates expressing the maximal available combination of virulence genes (today at minimum 1…11). Use of mix of three vital isolates reduces quantitative interaction clone/isolate. Last years isolates were collected on foliage blight-assessment field from clones infested at the end of season and attacking in single leave test differentials R5, R8, R9 too (avr1-avr11). These were cultivated for inoculation in following year.
4. Staggered applying of different assessment methods of foliage- and tuber blight resistance to consider specific influence as well of environment and plant age as tissue-specific expression of resistance (in tuber blight), and use of different criterions of resistance (see 4.2 and 4.4.).
5. Not to strong selection, decision on basis of several years average. Make compromises depending from breeding stage and genetic distance, flexible adaptation of limits for selection according to the breeding stage.
6. Choice of cross parents considers all known traits from the beginning (among wild clones, and in each progeny from seedling on, as possible); the desired trait combination depends from demand for the partner and the heritability. Succession of 7-8 generations has to be analysed from the end, the new, more resistant cultivar to relate desired trait expression to each breeding stage.
7. Crosses resistant x resistant have to be preferred as soon as the whole of traits enable it and sufficient variability can be expected. Pollen sterility is more common in interspecific progeny and because of chromosome imbalances frequently in following generations too and has to be counteracted (see 5.6, 6.1.).
8. A broad basis of pre-breeding clones from different species of *Solanum* and different accessions in it are developed to protect against adaptation of pathogen population by point 7 with genetic diversity of resistance and improved interaction of resistance genes.
9. Consequently local separation of growing for seed potato production from assessment of traits is realised after A-clone stage. Elimination of diseased plants is necessary at the beginning of its recognition.

Undivided and permanent responsibility of one person for both parts, breeding and pathology, led to development of described concept during first about 10 years and led to practical success in the very difficult task of pre-breeding for quantitative late blight resistance.

6.5.1. Priority of resistance to *P. infestans* over other traits

Seedlings selection on foliage and tubers realizes priority of blight resistance in pre-breeding (table 40), at which the risk is accepted to lose some resistant clones because of interaction resistance/plant age and environment. Continuity of tests in successive years evaluates blight resistance in different environmental conditions with different methods. Tuber slice test started in first year of growing in the field, single leaflets are assessed from second year on, field assessment of foliage blight resistance and whole tuber test begin in third field growing for three years each. Compromises concerning the other traits are made above all in connection with overcoming of barriers of fertility or to combine genetic very different material.

6.5.2. Combination of foliage and tuber blight resistance

Improved level of tuber blight resistance is regarded as key for effective use of foliage blight resistance at Gross Luesewitz. Quantitative tuber blight resistance passes for independent trait besides foliage blight resistance, because of tissue-specific expression of resistance; each level on foliage can be combined with each level on tubers (table 3). For that reason we choice sources of resistance with high level on foliage and tubers. At the beginning of our pre-breeding

even resistance of tubers has had highest priority at IK Gross Luesewitz. If resistance of tubers is the first trait of selection concerning late blight, the probability of wrong decision in breeding is smaller because of lower correlation to maturity as already mentioned Toxopeus (1958). Utilization of wild sources without high resistance of tubers lays the foundation-stone of failure, if breeder's collection does not contain excellent inheritors for tuber blight resistance. The expected advantage of such "new" sources for quantitative resistance (Colon 1994) is illusion.

6.5.3. Use of foliage blight resistance uncorrelated to maturity as true resistance

The range of maturity in our late blight resistant pre-breeding material is shown in figure 97, depending from breeding stage (wild species to BC5). Clones of BC3-BC5 give of dominating second early maturity with an early part (fig. 98). Under 2.5., 2.7. and 4.2.4. the own methodical solution is explained. The results in table 44 and figures 27-30 show that conventional breeding by empirical method can separate lateness effect from polygenic resistance. Improving of maturity by 2.4 scores simultaneously was reached to progress in combining resistance to *P. infestans* with culinary quality, suitability for processing or high starch content (Darsow 1999, 2002b, 2003b, 2005a, b, 2006) within about 30 years, without reduction of foliage blight resistance of pre-breeding material (table 44). Evidence is given in chapter 6.5.4-6.5.6 and 7. A second early, quantitatively late blight resistant clone bred nearly 25 years ago is BAZ-GL-94.7082.15 P Sp Po Kr1 Kr18 V (fig. 99).

Table 44 Percentage (%) of B- to D-clones of ZL with high foliage blight resistance in the field in classes of maturity over time.

Maturity	1973-75	1976-80	1981-85	1986-90	1991-95	1996-98	1999-2003	2004-06
7.5-9.0	0	0	0	0	0	1	1	1
6.5-7.4	0	0	1	0	4	7	2	8
5.5-6.4	0	0	4	1	9	14	9	24
4.5-5.4	0	3	9	4	16	20	28	33
3.5-4.4	7	9	41	34	38	30	34	22
2.5-3.4	48	85	39	57	32	27	25	12
<2.5	45	3	6	4	1	1	1	0
Maturity of main standard varieties								
Adretta	7.0	6.8	6.7	6.7	6.8	6.7	6.6	6.6
Mariella	3.5	3.4	3.3	3.3	3.2	3.3	3.3	-

Heritability coefficients for foliage blight resistance based on rAUDPC are given for population B of CIP with 0.41-0.71 (Landeo & Gastelo 1999). Genetic variance of foliage blight resistance, calculated according to Darsow & Strahwald (2006, unpublished), was smaller ($h^2 = 0.662$) than for rAUDPC ($h^2 = 0.778$). Calculation for 335 pre-breeding clones, tested two to four years in 2001-2004, showed heritability of $h^2 = 0.768$ for foliage resistance and $h^2 = 0.850$ for rAUDPC (resistance + maturity). In this pre-breeding material foliage blight resistance was calculated with the old (FBR_{GL}) method and by regression in parallel (see 4.2.3., 4.2.4.), showing that results of both correlated between r = 0.86 and r = 0.94 in different years. This result explains unique success in pre-breeding at Gross Luesewitz in past and establishes the suitability of the regression-method at the same time to combine quantitative resistance to foliage blight and

early maturity. The advantage of the regression-method is to be mathematically based and easy understandable. With its application it is possible to select really for foliage blight resistance. Beyond that, the improper use of the term resistance for differences in disease level can finally be finished; the term resistance can correctly be reserved for true resistance by maturity-correction of data of attack.

For the InnoNet-project TASK (see 8.2., table 69) four populations were assessed for foliage blight resistance in the field 2004-2006 with two replications of three plants each, inoculation with virulence gene combination avr1-avr11; cross parents were assessed in parallel with three replications, standard cultivars with eight, differentials (r-11) with one replication. Data of foliage blight resistance, calculated according to Darsow (1989b), and data of maturity are presented for season 2004 of the four populations (fig.100, see fig. 29, fig. 30). Very high variability exists for quantitative resistance of the populations in excellent manner. Foliage blight resistance correlated with maturity r = 0.046 in 2004, calculated for all populations together! Results of the other years were very similarly.

Pre-breeding clones with combined late blight resistance and earliness have to flower for following use for crossing. That is a problem as is visible in following data. A-clones grown in 2001 were 9% early, 56% second early and 35% second late. However, among the early ones 80% did not flower and 18% sparsely; in 265 second early clones 28% did not flower and 49% sparsely. Such trait correlation requires additional increased size of pre-breeding material. Simakov et al. (2008) expect to need 2-3 generations to select early varieties with increased polygenic foliage blight resistance.

6.5.4. Combination of late blight resistance with quality

6.5.4.1. Combination of late blight resistance with suitability for processing

Suitability for processing was absent in the sources of blight resistance used so far and has been assessed since 1993. Suitability for crisps as well as for French fries we had to introduce from *tbr*-gene pool. Samples are assessed for discolouration during processing immediately from storage at 4°C without reconditioning. Only clones with oval to long shape are tested for French fries. Improving of traits for processing was prepared in a project of potato quality since middle of 1980ies by H. Tiemann on diploid and tetraploid level. A part of development of good dihaploid parental clones for French fries is shown in table 45.

Table 45 Percentage (%) of dihaploid B- und C-clones in score-classes of discolouration of French fries from cold storage (4°C, Darsow & Tiemann, 2000).

		Scores for colour of French fries (9: bright golden, 1: black brown)								
Year of assessing	Number of clones	9	8	7	6	5	4	3	2	1
1992	250	0	0	1	5	21	28	24	16	5
1993	49	4	6	18	29	23	18	2	0	0
1994	68	0	15	18	21	19	16	9	0	2
1995	47	0	11	11	15	28	23	10	2	0
1996	42	0	0	17	24	33	21	5	0	0
1997	73	0	0	31	39	23	7	0	0	0
1998	85	4	8	31	42	10	5	0	0	0
1999	107	4	18	23	27	13	13	2	0	0

In 2000 75 tetraploid and 80 dihaploid clones were assessed as B- to D-clones in the sub-pro-

gramme blight resistance/processing, 517 as A-clones and 1400 single hills. After harvest 2006 15 tetraploid blight-resistant pre-breeding clones with suitability for processing were in stock (table 46).

Table 46 *Phytophthora*-resistant, tetraploid clones of ZL suitable for processing from cold storage (4°C). Results are three to four years average.

BAZ-GL-	French fries	Crisps	Starch content	Overall impression	Tuber shape long	Tuber size	Roughness of skin	Maturity	Foliage blight	Tuber resistance
93.7006.02	7.6	6.0	21.1	6.5	5.5	5.8	4.8	4.3	8.0	6.0
94.7222.13	8.0	4.3	22.0	6.7	6.0	5.5	6.5	3.0	7.9	6.3
94.7222.71	7.0	5.8	20.1	6.5	5.3	6.0	6.0	3.2	7.1	7.3
94.7231.14	7.0	4.9	19.9	7.0	5.0	5.7	5.2	4.3	6.8	7.3
96.7421.17	7.0	7.3	21.3	6.5	4.5	6.9	5.8	3.0	7.1	7.9
97.7550.07	7.0	4.0	19.7	6.7	4.0	6.3	4.8	3.8	6.9	7.7
98.7742.01	7.3	6.3	18.4	6.0	6.0	5.8	5.6	4.1	6.9	7.5
99.7930.02	7.0	6.5	22.5	5.8	5.7	6.4	4.5	4.0	8.3	8.0
00.1088.17	7.7	5.8	22.0	7.2	4.5	6.7	6.0	5.1	5.8	8.5
00.1106.04	7.0	6.0	21.9	6.9	5.8	6.2	5.0	3.7	5.8	8.1
00.1106.08	7.0	6.0	20.4	6.1	5.7	6.0	6.0	5.1	5.7	6.2
00.1163.06	7.0	5.3	22.5	6.0	4.5	5.4	5.2	5.4	5.3	7.3
01.1286.15	8.0	7.0	17.8	5.7	5.0	5.0	6.0	6.8	5.0	8.9
01.1303.05	7.5	4.3	22.7	7.0	4.7	6.7	4.3	4.5	5.0	6.5
01.1569.02	7.0	6.3	25.8	6.5	6.3	6.2	5.5	3.6	5.9	8.7

Score 9 = best expression. Tuber shape (alongside): 3 = round, 5 = oval, 7 = long, 9 = falcate.

All 15 clones were suitable for French fries according to their browning during frying, but only six were long enough as in figure 101 and figure 102, only four made large tubers. Two clones were good chippers (score ≥7, fig. 103); additionally eight with score ≥ 5.8 were limited useful cross parents (fig. 104). Eight of these clones were intended to use in sub-programme starch. Maturity of these blight-resistant processing-clones varies from early to second late. In some cases foliage blight resistance was below score 6 and a compromise for selection of parents for inter-crossing resistant x resistant. Present results prove real possibility of combining quantitative blight resistance with good processing traits in pre-breeding which should lead to breeding of cultivars with improved blight resistance suitable for processing in near future. Clone BAZ-GL-01.1293.01 P St Po with long tubers and netted skin means a good step to the trait combination for French fries (fig. 105).

For two of the clones in table 46 the pedigrees are written among pedigrees 8 in the following. Clone BAZ-GL-99.7930.02 P St Ch Po Tt Kr1 Ro1 and a parent of BAZ-GL-03.5118.09 P Sp Po were handed over to variety breeders. No one of the five clones with pedigrees 8 is late, but one is early and two are second early. All five include genes from *S. stoloniferum* additionally to *S. demissum*. Only BAZ-GL-02.5029.13 P Sp Po Kr1 Ro1 (fig. 106, pedigree 8.2.) includes Agria in its descent. BAZ-GL-03.5059.05 P St Ch Ro1 on the left side of figure 107 got score 7 for browning of crisps, but BAZ-GL-03.5118.09 P Sp Po on the right side proved to be not sufficiently suitable for production of crisps. Both pedigrees are to find in 8.3. and 8.5. Clone BAZ-GL-00.1106.04 P Sp Ch listed in table 46 is shown in figure 58 and pedigree 8.4. A sister is represented in figure 108. Bigger and longer tubers for French fries would be desired for the nice BAZ-GL-02.1412.02 P Sp Po (fig. 109), BAZ-GL-01.1577.06 P (Ch) Po Ro1 (fig. 110), and BAZ-GL-01.1272.03 P Sp Po Ro1 (fig. 111), both latter with smooth skin. The clones listed in pedigree 8.2 and 8.5. are shown in figure 112 with its French fries.

Pedigrees 8:

1. *sto* x Erika (1 *dms* 3.12%)
x Falke (1 *dms* 3.12%)
x Aquila (1 *dms* 3.12%)
x Eva (1 *dms* 2.54%)
x GL-I-62.356.11 ♀ (2 *dms* 2.73 %, *acl*)

dms 1947 x *dms* Reddick 52.20.154
x Amsel (1 *dms* 1.56%)
x Axilia (1 *dms* 1.56%, adg)
x Sitta (1 *dms* 3.90%)
x MPI 44.335.130 (1 *dms* 6.25%, *adg*)

x GL-VI-78.6701.01 (3*dms* 3.5%, *adg*)
x Rebecca (2-3 *dms* 5.66%, *adg*, *cmm*, *mag*)

BAZ-GL-99.7930.02 P St (22.6%) Ch Po Tt Kr1, Ro1, 5 se-sl (4-5 *dms* 5.08%, *acl*, *adg*, *cmm*, *mag*, *sto*)

2. *dms* PI 160 227 x *dms* Reddick 52.20.154
x Amsel (1 *dms* 1.56%)
x Axilia (1 *dms* 1.56%, *adg*)
x GL-I-64.644.04 (2 *dms* 2.73%, *adg*)
x Commandeur (1 *dms* 3.12%, *phu*)
x GL-III-70.326.35 (3-4 *dms* 3.5%, *adg*)
x Adretta (2 *dms* 2.92%, *adg*)

sto x Erika (1 *dms* 3.12%)
x Zuchtstamm (1 *dms* 1.56%)
x MPI 44.1016.10X (*acl*)
x Zuchtstamm (1 *dms* 1.56%, *adg*)
x GL-III-70.326.35 (3-4 *dms* 3.5%, *adg*)

x Beluga (1-2 *dms* 1.4%, *adg*)

BAZ-GL-02.5029.13 P Sp Po Kr1, Ro1 ea (6 *dms* 2.42%, *acl*, *adg*, *phu*, *sto*)

3. *dms* PI 160 227 x *dms* Reddick 52.20.154
x Amsel (1 *dms* 1.56%)
x Axilia (1 *dms* 1.56%, *adg*)
x GL-I-64.644.04 (2 *dms* 2.73%, *adg*)
x Commandeur (1 *dms* 3.12%, *acl*)
x GL-III-70.326.35 (3-4 *dms* 3.5%, *adg*)
x Adretta (2 *dms* 2.92%, *adg*)
x GL-I-82.037.181 ♀ (2 *dms* 2.92%, *adg*)

dms PI 160 227 x *dms* Reddick 52.20.154
x Amsel (1 *dms* 1.56%)
x Axilia (1 *dms* 1.56%, *adg*)
x GL-I-64.644.04 (2 *dms* 2.73%, *adg*)
x Commandeur (1 *dms* 3.12%, *acl*)
x GL-III-70.326.35 (3-4 *dms* 3.5%, *adg*)
x Adretta (2 *dms* 2.92%, *adg*)
x GL-VI-78.6734.35 (*sto* 1.56%, *dms* 3.22% *acl*, *adg*, *phu*)

BAZ-GL-03.5118.09 P Sp Po se (6 *dms* 3.80%, *acl*, *adg*, *phu*, *sto*)

4. *dms* PI 160 227 x *dms* Reddick 52.20.154
x Amsel (1 *dms* 1.56%)
x Axilia (1 *dms* 1.56%, *adg*)
x Sitta (1 *dms* 3.9%, *adg*)
x MPI 44.335.130 (1 *dms* 6.25%, *adg*)
x GL-I-72.102.122 (2 *dms* 2.68%, *acl*, *adg*, *sto*)
selfing
x Tessi (*dms* 0.78%)

BAZ-GL-00.1106.04 P St (21.9%) (Ch) Po Kr1 Ro1se-sl (3-4 *dms* 3.24%, *acl*, *adg*, *sto*)

5. mix *tbr* (1.56% *dms*) x mix *sto* GLKS **4**, **22**, **23,** several accessions each
x GL-I-67.269.05 (2 *dms* 2.92%, *adg*)
x Rebecca (2-3*dms* 5.66%, *adg*, *cmm*, *mag*, *sto*)
x Delikat (1 *dms* 2.05%, *adg*)

BAZ-GL-03.5059.05 P Sp Po Ro1se (1 *sto* 6.25%, 3 *dms* 2.9%, *adg*, *cmm*, *mag*)

6.5.4.2. Combination of late blight resistance with table potato quality

Combining of quantitative resistance of foliage and tubers to late blight from wild species with table potato quality is very difficult because of the great complex of involved traits. Slow development in intervals of four to seven years is shown for the sub-programme in table 47. Results of third to fifth year of growing in field characterize in average each clone. According to the year of sowing mean value of each clone is assigned to suited interval.

Table 47 Changing of traits of table potato quality of late blight resistant pre-breeding clones of backcross step 4 (BC4) during 25 years at ZL. Three years average of all clones of the sub-programme is included according to year of sowing in mean value of interval 1977-1981, 1982-1987, 1988-1995, 1996-1999, 2000-2003).

Year of sowing	1977-81	1982-87	1988-95	1996-99	2000-03
Foliage blight resistance (1-9)	6.1	6.7	6.9	7.7	7.4
Tuber blight resistance (1-9)	7.9	7.5	7.1	7.0	7.4
Index table quality (1-9)	3.0	4.1	4.2	4.8	5.7
Cooking type (A-D) average	D	D	D	CD-C	BC-C
Appearance after cooking (1-5)	2.6	2.8	3.1	3.1	3.6
Discolouration after cooking (1-9)	3.7	3.8	3.7	4.8	5.4
Disintegration during cooking (1-5)	2.9	3.1	3.4	3.3	3.6
Consistency after cooking (1-5)	3.0	3.1	3.1	3.3	3.6
Mealiness (1-5)	2.8	2.9	2.9	3.0	2.9
Taste (1-5)	2.9	3.1	3.2	3.1	3.2
Blue bruise (1-9)	3.5	3.4	4.3	4.8	5.3
Colour of tuber flesh (1-9)	3.7	4.1	4.6	4.4	4.2
Roughness of skin (1-9)	3.9	4.2	4.9	5.3	5.8
Part of cracked tubers (%)	5.7	5.9	3.4	2.5	1.2
Tubers with internal rust spot (%)	3.2	2.8	3.1	1.4	1.0
Part tubers with hollow heart (%)	8.0	3.3	5.2	7.0	1.8
Number of clones	21	44	75	26	32

Highest score (9 or 5, respectively): best possible expression. Cooking type A: firm, B: a little mealy to firm, C: mealy, D: strongly disintegrating during cooking.

Averages indicate only little change concerning mealiness and taste during 20 years. Culinary index or index of table potato quality was improved to a nearly sufficient level. Cooking type was changed from D to nearly BC, i.e. from strongly disintegrating during cooking to a little bursting, not disintegrating state. Breeding progress can be stated concerning appearance after cooking (fig. 113), discolouration after cooking (fig. 114), disintegration during cooking (fig. 113), consistency, resistance against blue bruise (fig. 115), colour of tuber flesh and roughness of skin. External and internal defects as cracked tubers, internal rust spots, and hollow heart could be decreased. All these changes occurred in spite of increase of foliage blight resistance and a little decrease of tuber blight resistance.

Table 47 shows tendency of progress in pre-breeding in average of tested clones. In 2006 some clones played an important part as cross parents due to its especially successful combination. Six such clones are described in table 48 with abbreviated clone number. The lower the back-

cross number, the higher is the part of wild alleles in it. Sources of blight resistance in it are *Solanum circaeifolium* (*crc*), *S. okadae* (*oka*), *S. demissum* (*dms*) and *S. stoloniferum* (*sto*). Already in first or second backcross (BC1 or BC2, respectively) clones with intermediate to good culinary traits were found. This new situation opens larger margin for crosses (*P. infestans*-resistant + table potato quality) x (*P. infestans*-resistant + table potato quality). Index of table potato quality, cooking type and discolouration after cooking are in these cases satisfactory to good. Very high foliage blight resistance of number Z3601 and 7419 involve the risk of unknown R-gene effect. Clones 264 and 7784 do not come up with cultivar Leyla, however, they are suitable cross parents for the subprogramme 'late blight resistance and table potato', being second early respectively early, middle or highly resistant and near cultivar level of quality traits. This combination did not succeed anywhere till now. In patient long-term breeding we overcame difficulties and show combinability of quantitative blight resistance with earliness and complex quality traits – contrary to all expectations (Allefs et al. 2005). Nevertheless, our pre-breeding is on the right way, but the goal is not reached, biological possibilities of further improvement has to be exploited with small steps.

Table 48 Currently used parental pre-breeding clones for resistance to *P. infestans* and culinary quality in 2006 at ZL. Highest score (9 or 5 respectively): best possible expression, very early, respectively. Cooking type A: firm, B: a little mealy to firm, C: mealy, D: strongly disintegrating during cooking.

Breeding clone (short number)	7557	Z3601	7579	7419	264	7784	Leyla
Backcross stage	BC1	BC1	BC3	BC2	BC4	BC4	Standard
Wild species as donors of resistance	*sto*	*crc*	*sto*	*oka*	*dms*	*dms*	-
Foliage blight resistance (1-9)	8.8	8.8	8.1	8.9	7.3	7.4	2.8
Whole tuber blight resistance (1-9)	7.6	7.9	8.7	7.1	6.8	9.0	4.7
Index of table potato quality (1-9)	6.6	3.0	5.4	7.1	5.6	6.2	6.2
Cooking type (A-D)	C	A	B	BC	C	C	AB
Appearance after cooking (1-5)	3.4	3.7	3.5	4.3	3.3	3.5	4.1
Taste (1-5)	3.6	2.8	3.5	3.7	3.3	3.0	3.4
Discolouration after cooking (1-9)	7.0	4.0	5.0	6.0	5.5	8.0	5.3
Disintegration during cooking (1-5)	3.6	4.2	3.5	3.6	4.0	3.5	4.5
Consistency after cooking (1-5)	3.5	4.3	4.0	4.3	3.8	3.5	4.0
Mealiness (1-5)	2.9	4.0	4.0	3.3	3.0	3.0	3.8
Resistance against blue bruise (1-9)	4.0	5.3	3.0	6.6	5.2	5.8	6.3
Colour of tuber flesh (1-9)	4.8	4.2	3.7	6.3	4.5	5.4	6.7
Part of cracked tubers (%)	2	0	0	0	6	0	0
Tubers with internal rust spot (%)	0	0	0	3	0	0	1
Part tubers with hollow heart (%)	5	0	2	0	8	0	1
Maturity (1-9, 9 = very early)	3.7	4.5	4.1	5.9	4.5	6.5	6.8
Roughness of skin (1-9)	6.2	6.5	6.2	5.8	6.3	6.0	7.2

Clone 7419, 264 and 7784 were offered to variety breeders. Descent of more young pre-breeding clones is shown under Pedigrees 9. Two clones from S. okadae expressed sufficient table potato quality in an early breeding stage (pedigree 9.1). A similar clone is shown in figure 116: BAZ-GL-01.1467.01 P (Sp Ch) Ro1, a B2 from S. okadae. Very high quantitative blight resistance is combined with good table quality in pedigree 9.2. in mealy cooking type with rough skin and good virus resistance. BAZ-GL-02.1412.02 was expected to be preferred cross parent in 2007. BAZ-GL-99.8095.01 was handed over to variety breeders in 2005, BAZ-GL-99.8084.01 in 2006 (fig. 117, pedigree 9.6.). BAZ-GL-03.5115.05 includes S. circaeifolium, both parents possess table quality. BAZ-GL-00.8069.01 combined own with Russian gene pool; the own mother is a tetraploid selection from production of dihaploids with S. phureja.

Pedigrees 9:

1. *oka* BGRC 028970 + GL-VI-87.089.32 diha (1 *dms* 1.56%, *adg*)
   - x Pamir (*dms* 0.78%, *adg*)
   - x Leyla (0.94% *dms*, *adg*, *chc*)
   - x Granola (*dms* 1.56%, *adg*)
   - x Likaria (2 *dms* 1.6%, *adg*)

   BAZ-GL-01.1465.03 P Sp Ro1, 5 ea-se (1 *oka* 12.5%, 1-2 *dms* 0.86%, *adg*, *chc*)

   BAZ-GL-03.5067.04 P Sp Ro1 ea-se (1 *oka* 12.5%, 2 *dms* 1.36%, *adg*)

2. *dms* PI 160 227
   - x *dms* Reddick 52.20.154
     - x Amsel (1 *dms* 1.56%)
     - x GL-I-62.110.13 (1 *dms* 1.56%, *adg*)
     - x Axilia (1 *dms* 1.56%, *adg*)
     - x GL-I-65.774.105B (2 *dms* 2.88%, *adg*)
     - x Adretta ♀ (2 *dms* 2.92%, *adg*)
     - x S. *phureja*

   dms PI 160 227
   - x *dms* Reddick 52.20.154
     - x Amsel (1 *dms* 1.56%)
     - x Axilia (1 *dms* 1.56%, *adg*)
     - x Commandeur (1 *dms* 3.12%, *phu*)
     - x GL-III-70.326.35 (3-4 *dms* 3.5%, *adg*)
     - x Adretta (2 *dms* 2.92%, *adg*)
     - x GL-VI-78.6734.35 (*sto* 3.12%, 3-4 *dms* 2.92%, *acl*, *adg*, *phu*)

   BAZ-GL-01.1395.01 P Sp ea (6 *dms* 4.43%, *sto* 1.56%, *acl*, *adg*, *phu*)

3. *dms* PI 160 227
   - x *dms* Reddick 52.20.154
     - x GL-VI-60.2871.135 diha (1 *dms* 1.56%)
     - x GL-I-64.644.04 (2 *dms* 2.73%, *adg*)
     - x GL-I-65.774.105B (2 *dms* 2.88%, *adg*)
     - x GL-II-71.696 (1 *dms* 1.56%, *acl*, *adg*)
     - x GL-VI-82.9269.10XY (1-2 *dms* 1.75%, *adg*)

   dms PI 160 227
   - x *dms* Reddick 52.20.154
     - x Amsel (1 *dms* 1.56%)
     - x GL-I-62.110.13 (1 *dms* 1.56%, *adg*)
     - x Axilia (1 *dms* 1.56%, *adg*)
     - x GL-I-65.774.105B (2 *dms* 2.88%, *adg*)
     - x MPI 44.335.130 (1 *dms* 6.25%, *adg*)
     - x GL-VI-78.6706.01 ♀ (3 *dms* 3.5%, *adg*)

   BAZ-GL-02.1412.02 P Sp Po Kr1ea-se (5 *dms* 5.18%, *acl*, *adg*)

4. *dms* PI 160 227
   - x *dms* Reddick 52.20.154
     - x GL-VI-60.2871.135 diha (1 *dms* 1.56%)
     - x GL-I-64.644.04 (2 *dms* 2.73%, *adg*)
     - x GL-I-65.774.105B (2 *dms* 2.88%, *adg*)
     - x GL-III-70.326.35 (3-4 *dms* 3.5%, *adg*)
     - x Tewadi (1-2 *dms* 2.64%, *adg*)

   dms PI 160 227
   - x *dms* Reddick 52.20.154
     - x Amsel (1 *dms* 1.56%)
     - x Axilia (1 *dms* 1.56%, *adg*)
     - x GL-I-64.644.04 (2 *dms* 2.73%, *adg*)
     - x Commandeur (1 *dms* 3.12%, *phu*)
     - x GL-III-70.326.35 (3-4 *dms* 3.5%, *adg*)
     - x Adretta (2 *dms* 2.92%, *adg*)

   x Leyla (2-3 *dms* 0.94%, *adg*, *chc*, *vrn*)

   BAZ-GL-99.8095.01 P Sp Tt Kr1 Ro1 V se (6 *dms* 2.68%, *acl*, *adg*, *chc*, *phu*, *vrn*)

5. *dms* PI 160 227
   - x *dms* Reddick 52.20.154
     - x GL-VI-60.2871.135 diha (1 *dms* 1.56%)
     - x GL-I-64.644.04 (2 *dms* 2.73%, *adg*)
     - x GL-I-65.774.105B (2 *dms* 2.88%, *adg*)
     - x GL-II-71.696 (1 *dms* 1.56%, *acl*, *adg*)
     - x GL-VI-82.9269.10XY (1-2 *dms* 1.75%, *adg*)

   crc BGRC 27034 + H 256 diha
   - x Irmgard ♀ (1 *dms* 0.59%, *adg*, *sto*, *vrn*)
   - x Pamir (1-2 *dms* 078%, *adg*)

   BAZ-GL-03.5115.05 P Sp Ro1 se (1 *crc* 6.25%, 4 *dms* 2.8%, *acl*, *adg*, *sto*, *vrn*)

6. *dms* PI 160 227 x *dms* Reddick 52.20.154
   x Amsel (1 *dms* 1.56%)
   x GL-I-62.110.13 (1 *dms* 1.56%, *adg*)
   x Axilia (1 *dms* 1.56%, *adg*)
   x GL-I-65.774.105B (2 *dms* 2.88%, *adg*)
   x Adretta ♀ (2 *dms* 2.92%, *adg*)
   x Rebecca (2-3 *dms* 5.66%, *adg*, *cmm*, *mag*)
   x Leyla (2-3 *dms* 0.94%, *adg*, *chc*, *vrn*)
   BAZ-GL-99.8084.01 P Sp Tt Kr1 Ro1 ea-se (5 *dms* 3.29%, *acl*, *adg*, *chc*, *cmm*, *mag*, *vrn*)

7. *dms* PI 160 227 x *dms* Reddick 52.20.154
   x Amsel (1 *dms* 1.56%)
   x GL-I-62.110.13 (1 *dms* 1.56%, *adg*)
   x Axilia (1 *dms* 1.56%, *adg*)
   x GL-I-65.774.105B (2 *dms* 2.88%, *adg*)
   x Adretta ♀ (2 *dms* 2.92%, *adg*)
   x *S. phureja*
   x Berezka (2-3 *dms* 2.3%, *adg*)
   BAZ-GL-00.8069.01 P Sp Kr1 V ea-se (4-5 *dms* 3.97%, *adg*, *phu*)

Additionally clone BAZ-GL-98.236.01 P Sp Ro1 Ro2 Ro3 Ro5 with netted skin has a nice oval tuber shape and is a good cross parent in the sub-programme for blight resistant table potatoes. Another good example is BAZ-GL-00.1143.07 P Sp Ro1.

6.5.4.3. Combination of resistance to *P. infestans* and *Globodera pallida* as well as *G. rostochiensis* with high starch content

An important utilization of potato crop means production of starch for food and industrial purpose. Although late maturing starch cultivars are mainly considered as blight-resistant on foliage, its fungicide demand is particularly high, for instance 9-12 applications compared with 5-7 in ware potatoes per year (Hansen et al. 2002a). Our sub-programme 'starch/late blight' in pre-breeding meets demand for blight-resistant, second early to second late parental clones with high starch content and resistance on foliage and tubers. New studies confirmed that tuber starch content is a quantitative and polygenic trait; genes contributing to the phenotypic effects are located on all chromosomes (Gebhardt et al. 2005).

Only at the middle of 1980ies starch content gained in significance in our pre-breeding (Darsow 2003b). The table 49 shows development in combining earlier maturity, foliage blight resistance and starch content. Maturity 3 means second late, 5 second early, score 7 corresponds with early. For starch content different percentage are fixed; each column gives the number of clones characterised by written class of maturity and resistance, but lower/coincident or higher starch content. At the beginning of the 1980ies the material was late or second late. One generation later first second early clones with blight resistance and better starch content were yielded. Two generations later first blight-resistant early starch-clones were bred.

Table 49 Number of pre-breeding clones of ZL with high foliage blight resistance and high starch content in classes of maturity (Score 9: highest level of resistance, very early).

	Maturity	<3	3	4	5	6	7
	Foliage blight resistance	>7	>7	>6.5	>6	>6	>6
Year of sowing	Starch content (%)	</>21	</>20	</>19	</>18	</>17	</>16
1981		1/1	1/0		0/1		
1982		1/1	5/4	2/1			
1983		2/0	4/1	2/0			
1984		4/0	14/1	3/0			
1985		3/2	1/0	1/0	0/1		
1986			2/0	6/0	3/0		
1987		1/0	6/0		2/1		
1988				2/1	2/0		
1989				1/0	0/3	1/0	
1990		1/0	7/0	5/0			
1991		2/2	7/1	2/1	0/3		
1992		3/0	3/1	2/3	2/1		
1993		4/3	0/7	0/8	0/5	0/5	
1994		2/0	2/7	2/8	4/8	0/3	
1995		1/0	2/0	2/2	2/1		
1996		3/0	4/2	3/2	2/3	2/0	
1997		3/2	6/2	7/5	0/1	2/2	
1998			5/0	4/0	7/1	1/2	1/0
1999		5/4	1/4	11/6	8/5		1/1

Pre-breeding for starch/late blight sub-programme was promoted since 2000 to 2003 by a national project at ZL. Besides other utilizations about 18,000 or 17,000 seeds were sown in 2001 and 2002. The combination of starch content, starch yield, foliage and tuber blight resistance with second early maturation was intended. Already in 2002 four clones were handed over to German enterprises of cultivar breeding (table 50, fig. 118-120). First and second clone in table 50, both are second early, the following ripe second late. High starch content is combined with high level of quantitative resistance to *P. infestans* on foliage and tubers. Three clones coincide with cultivar Tomensa concerning yield and starch content, but are characterized by an essentially higher late blight resistance. Clone BAZ-GL-94.7235.3 has best performance and additional suitability for French fries after cold storage at 4°C (fig. 119). Beyond that, three clones are pollinators, three possess high quantitative resistance to *Erwinia*-soft rot, and one is resistant to nematode Ro1, another to potato wart disease pathotype 1.

Table 50 Maturity, starch content and resistance to *P. infestans* on foliage and tubers of four clones handed over to cultivar breeders as cross parents in April 2002 (Score 9 = very early, highly resistant; all data present three years average).

	Maturity	Starch content (%)	Foliage blight resistance	Tuber blight resistance
BAZ-GL-93.7091.8	5.2	21.0	7.7	6.8
BAZ-GL-95.7286.1	4.7	20.3	7.0	7.6
BAZ-GL-93.6984.7	3.7	21.9	7.6	7.8
BAZ-GL-94.7235.3	3.1	23.0	7.7	8.0
cv. Tomensa for comparison	6.0	21.0	3.8	4.1

Parentages of younger clones are given under pedigrees 10. In 10.1. a late blight resistant new clone of *S. stoloniferum* is introduced and proved to contribute to high starch content. Very few seeds from single crosses *tbr* x mix of *sto* were put together to use late blight resistant and male fertile clones of *S. stoloniferum* in 10.2. Tolerance to drought seems to be supported by genes from Rebecca. The early maturing BAZ-GL-01.1293.01 includes genes from 5-6 different clones of *S. demissum*; tolerance to drought and improved resistance to soft rot (*Erwinia carotovora* ssp. *atroseptica*) are combined with high starch content and blight resistance. Its female cross parent is a tetraploid selection after crossing of the late blight resistant clone BAZ-GL-93.7006.02 with *S. phureja* to produce dihapoids, similarly in 10.4. Clone BAZ-GL-00.1195.13 combined starch content, resistance to late blight, soft rot and viruses; the clone is handed over to variety breeders in 2006. The second early clone BAZ-GL-01.1268.03 expresses high starch content with resistance against most pathotypes of *Globodera rostochiensis* and against late blight on foliage and tubers. Russian cultivar Loshitsky enlarged the gene pool by BAZ-GL-03.5127.01.

Pedigrees 10:

1. *sto* GLKS 68.**23**.62.05
   - x *adg* IPK **3**.2558
   - x mix *tbr* (*dms* 0.78%, *adg*)

   dms PI 160 227 x *dms* Reddick 52.20.154
   - x GL-VI-60.2871.135 diha (1 *dms* 1.56%)
   - x GL-I-64.644.04 (2 *dms* 2.73%, *adg*)
   - x GL-I-65.774.105B (2 *dms* 2.88%, *adg*)
   - x GL-II-71.696 (1 *dms* 1.56%, *acl*, *adg*)
   - x *S. phureja*

   BAZ-GL-99.7956.01 P St (23%) Po Kr1 sl-la (1 *sto* 12.25%, 4 *dms* 4.48%, *acl*, *adg*, *phu*)

2. tbr mix (*dms* 0.78%, *adg*)
   - x *sto* GLKS mix **4**, **22**, **23**
   - x Ilse ♀ (*dms* 1.17%, *adg*)
   - x Rebecca (2-3*dms* 5.66%, *adg*, *cmm*, *mag*)

   BAZ-GL-99.7985.02 P St (24%) Tt Kr 1 sl (1 *sto* 12.25%, 2-3 *dms* 3.22%, *adg*, *cmm*, *mag*)

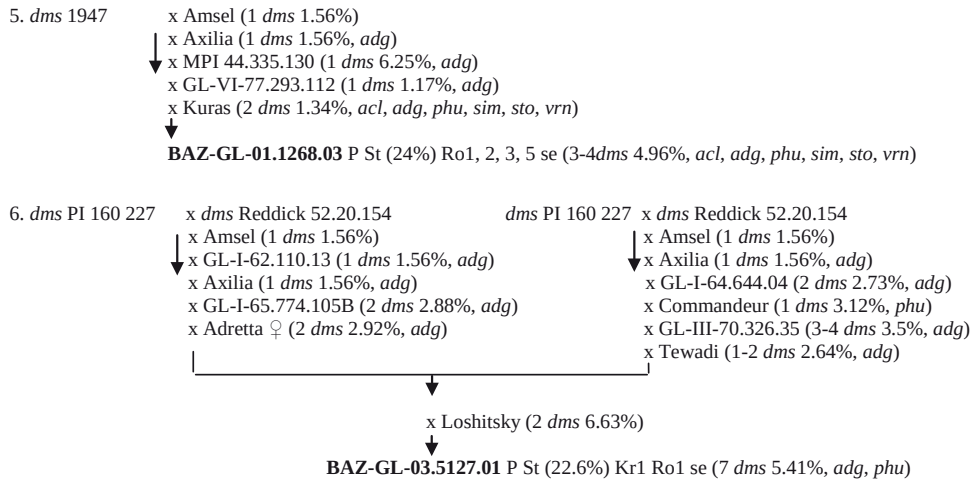
3. *dms* PI 160 227
   - x *dms* Reddick 52.20.154
   - x Amsel (1 *dms* 1.56%)
   - x GL-I-62.110.13 (1 *dms* 1.56%, *adg*)
   - x Axilia (1 *dms* 1.56%, *adg*)
   - x GL-I-67.269.05 (2 *dms* 2.92%, *adg*)
   - x GL-III-70.326.35 (3-4 *dms* 3.5%, *adg*)
   - x *S. phureja*
   - x BAZ-GL-93.7091.08 (3-4*dms* 4.43%, *adg*, *cmm*, *mag*)

   BAZ-GL-01.1293.01 P St (21.2%) Tt Kr1 Eca ea (5-6 *dms* 5.18%, *adg*, *cmm*, *mag*, *phu*)

4. *dms* PI 160 227
   - x *dms* Reddick 52.20.154
   - x Amsel (1 *dms* 1.56%)
   - x GL-I-62.110.13 (1 *dms* 1.56%, *adg*)
   - x Axilia (1 *dms* 1.56%, *adg*)
   - x GL-I-65.774.105B (2 *dms* 2.88%, *adg*)
   - x Adretta (2 *dms* 2.92%, *adg*)
   - x *S. phureja*

   dms PI 160 227 x *dms* Reddick 52.20.154
   - x Amsel (1 *dms* 1.56%)
   - x Axilia (1 *dms* 1.56%, *adg*)
   - x GL-I-64.644.04 (2 *dms* 2.73%, *adg*)
   - x Commandeur (1 *dms* 3.12%, *phu*)
   - x GL-III-70.326.35 (3-4 *dms* 3.5%, *adg*)
   - x Adretta (2 *dms* 2.92%, *adg*)
   - x GL-VI-78.6734.04 (3-4 *dms* 3.22%, 1 *sto* 3.12%, *acl*, *adg*)

   BAZ-GL-00.1195.13 P St (20.3%) Eca V ea- se (6 *dms* 4.19%, 1 *sto* 1.56%, *acl*, *adg*, *phu*)



The white potato cyst nematode *Globodera pallida* Stone is in Germany important in regions of starch potato production by drag in with seed potatoes and because of disregarding of crop rotation cycle of at least four years. Cysts in soil contain viable eggs about ten years. Ecologically beneficial plant protection includes sanitation measures and growing of cultivars resistant to *G. pallida*. Such cultivars in past reacted as poor hosts; they could decrease high population density to about 50%, whereas low densities could not be farther reduced (Mulder & Brinkmann 1996). Breeding intends continue to improve level of resistance against pathotype Pa2 and Pa3, which is determined by several genes. Besides resistance high tolerance against infestation proved to be useful which results in lower depression of growth and yield (Lauenstein 1998). This additional trait seems to be determined by polygenes (Arntzen et al. 1994).

Following cultivars, breeding clones and wild clones of gene bank were used in ZL Gross Luesewitz as sources of resistance to white cyst nematode *G. pallida* pathotype 2 and 3: Kardent, Stabilo, Kartel and Dorett, dihaploid clones BAZ-GL-86.8485.29, BAZ-GL-86.8489.205, which trace back to *S. gourlayi*, BAZ-GL86.625.01 (4x), BAZ-GL-94.169.04 (2x), which go back to *S. spegazzinii*, Cebeco DH 84.161257, Cebeco RH 89.22.10, Cebeco 3778.16, diploids GLKS 99.002.798.255, GLKS-99.002.798.256, GLKS-99.002.798.257, GLKS-99.002.798.258, GLKS-99.806.001 from *S. vernei*, GLKS-99.061.941.266, GLKS-99.061.953.001, GLKS-99.061.971.271, GLKS-99.061.971.273, GLKS-99.061.975.279 from *S. sparsipilum*, GLKS-99.160.2746.001, GLKS-99.160.2759.298, GLKS-99.160.2759.300, GLKS-99.160.2759.301 and GLKS-99.160.2772.319 from *S. spegazzinii*. The GLKS-clones were taken over in 2001.

In 2003 51 new dihaploid cross combinations were sown. Nine dihaploid and 28 tetraploid clones showed high resistance against *G. pallida*, partly combined with suitability for processing. Cross parents with different genetic background were combined, cultivars with highest resistance and tolerance to Pa2 and Pa3 were preferred. Besides crossing a programme with 70 fusion combinations was started.

Some cross parents resistant to *G. pallida* and grown in 2006 in ZL are listed in table 51. Five of the nine clones express high late blight and nematode resistance combined with high starch content and second early to second late maturity. Going on with this material seems tempting and promising to contribute to new starch varieties with resistance to *G. pallida*, improved late blight resistance and earliness. Figure 121 shows clone BAZ-GL-00.1076.10 P Pa2 Pa3 St ea of this programme combining earliness with high starch content and resistance to late blight as

well as to Pa2 and Pa3. Clone BAZ-GL-01.1569.02 P Pa2 Pa3 St Ch with a bit rough skin and long oval tuber shape is listed in table 44 and 49 as well as presented in figure 122. One parent is variety Kartel. Progeny from crosses with variety Kardent usually possess very rough skin (fig. 123, BAZ-GL-00.1079.05 P St Pa2 Pa3).

Tolerance to infestation with *G. pallida* is considered for choice of parental cultivars till now in our pre-breeding only, not in assessment of pre-breeding material so far.

Table 51 Cross parents with resistance to *Globodera pallida* grown in the field 2006.

Clone BAZ-GL-	Species[1)] Ploidy Cross	Pa2	Pa3	Foli-age	Tuber	Starch content	Yield g per plant	Beauty of tubers	Maturity
		Cysts/pot		blight resistance					
00.1035.01	*spg*, F1, 2x	0	0	2.5	4.1	20.2	641	5.5	4.2
00.1076.18	*vrn*, 4x	2.7	6.2	5.4	6.7	19.2	863	6.9	4.6
00.1079.05	*vrn*, *adg*, 4x	0	0.2	5.3	6.7	20.4	1415	7.4	3.1
00.1113.02	*vrn*, 4x	0.3	0.8	6.0	7.9	22.3	1229	6.8	4.3
01.1332.02	*vrn*, *dms*, *sto*, F1	0	0	9.0	8.5	22.2	602	4.7	5.3
01.1342.02	*vrn*, *oka*, BC2	0.5	0	9.0	8.6	20.2	813	5.3	4.2
01.1343.01	*vrn*, *crc*, 4x	0.8	0.2	9.0	8.6	20.6	1433	5.5	4.0
01.1569.02	*vrn*, 4x	0.3	0	5.9	8.7	25.8	1232	7.0	3.6
01.1573.01	*oka*, B2, 4x	3.5	0.5	4.6	5.4	20.7	1208	5.2	2.8

[1)]: *adg* = *S. tuberosum* ssp. *andigena*, *crc* = *S. circaeifolium*, *dms* = *S. demissum*, *oka* = *S. okadae*, *spg* = *S. spegazzinii*, *sto* = *S. stoloniferum*, *vrn* = *S. vernei*.

Pedigree 11.1. and the middle example of 11.2. show consequent orientation to starch from the beginning. BAZ-GL-01.1573.01 should be used to go on in combining table quality with resistance to *G. pallida* and *P. infestans.*

Pedigrees 11:

1. *dms* GLKS 83.**10**.60.02 x *sto* GLKS mix **22**.2, 3, 6, 11, 22, 24
x Kardent (2 *dms* 3.12%, *adg*, *opl*, *phu*, *vrn*)

BAZ-GL-01.1332.02 P St (23.1%) Pa2 Pa3 se (3-4 *dms* 26.06%, 1 sto 25%, *acl*, *adg*, *phu*, *vrn*)

2. *oka* BRC 028969 + GL-VI-87.089.32

x Pamir (dms 0.78, adg)
x Dorett (dms 2.34%, adg, vrn)

x Panda (*dms* 3.12%, *adg*, *vrn*)
x Kardent (*dms*, *adg*, *opl*, *phu*, *vrn*)

x Granola (1-2 dms 1.17%, adg)
x Kardent (*dms*, *adg*, *opl*, *phu*, *vrn*)

BAZ-GL-01.1571.05 P (St 17.1%) Pa2 Pa3 Ro 1, 2, 3, 5 ea-se (1 oka 12.25%, *dms* 1.28%, *adg*, *vrn*)

BAZ-GL-01.1342.02 P St (20.2%) Pa2 Pa3 Ro1, 2, 3, 5 ea-se (1 oka 12.25%, *dms* 2.54%, *adg*, *opl*, *phu*, *vrn*)

BAZ-GL-01.1573.01 P Sp (Po) Pa2 Pa3 Ro1, 2, 3, 5 sl (1 oka 12.25%, 3 *dms* 2.14%,*adg*, *opl*, *phu*, *vrn*)

Late blight resistant clone BAZ-GL-01.1571.05 P (St) Pa2 Pa3 Ro1, Ro2, Ro3, Ro5 ea-se in pedigree 11.2. is a BC2 descending from *oka* with good tuber blight resistance (fig. 124). Three BC2-clones resistant to late blight and *G. pallida* are shown in figure 125 in successfully finished foliage blight assessment. BAZ-GL-01.1572.03 P Pa2 Pa3 and BAZ-GL-01.1572.02 P Pa2 are selected from (((*tbr* + *oka*) x Panda) x Dorett), and BAZ-GL-01.1446.01 P Pa2 Pa3 from ((((*dms* x *plt*) x GL-III-70.326.35) x GL-VI-82.6269.10XY) x GL-VI-90.6648.84.10).

Above mentioned diploid GLKS-clones were crossed with dihaploid clones of ZL (fig. 126). Parts of such seed populations were offered to cultivar breeding.

Resistance to *G. rostochiensis* can easily be added with last cross steps before selection of varieties. Therefore this trait has not a high priority in pre-breeding. However, it does not mean, it is not considered. Clone BAZ-GL-98.236.01 P Sp Ro1 Ro2 Ro3 Ro5 with netted skin and oval tubers is late blight resistant and resistant to four tested biotypes of the golden cyst nematode (fig. 127). Clone BAZ-GL-00.1143.07 P Sp Ro1 possesses high late blight resistance on foliage and tubers and shallow to very shallow eye depth (fig. 128).

6.5.5. Breeding on tetraploid and diploid level

Polygenic or oligogenic nature of the most important traits of potato requires in the pre-breeding material sufficiently broad genetic variability for breeding progress by combining. One of advantages of dihaploids is the necessity of much lower numbers of seedlings to find desired combinations. Earlier public potato breeding at Gross Luesewitz enabled a broad based dihaploid breeding programme over decades to support variety breeding (Tiemann 1989, 1991). Therefore in the 1990ies a broad assortment of inter-dihaploids of the second to fourth generation was available with cultivar-corresponding level (fig. 129), however, rarely with late blight resistance. Additionally, introduction of some Canadian breeding clones reduced in the following generation inbreeding depression, improved the type of plants, tuber size and yield, but decreased virus resistance level and possessed no any late blight resistance.

Compared with dihaploids derived from varieties such from late blight resistant hybrids were more difficult to produce and showed a more negative expression of cultivated traits and generally disturbed male fertility. Production of dihaploids from best late blight resistant clones of BC4-BC5 occurred yearly. Only backcrosses were possible so far or crossing with diploid wild clones susceptible on tubers. PD-clones (Trognitz et al. 2002) were one hope to improve fertility, but its blight susceptibility in long-day conditions gave reason for only few attempts to cross. The quantitative type of resistance in our material is shown in the progeny of a PD-cross (Fig. 100), the extreme lateness of the PD-clone at the same time. Only one clone was kept from crosses with PD in 2007 from ([(tbr diha x *spg*) x *ber*] x PD 149), in which an R-gene from *S. berthaultii* may cause the level of resistance. The restrictions from fertility reduced exploitation of the otherwise nice possibilities of trait combination (Ross 1966, Iwanaga 1984, Ortiz & Peloquin 1994). For instance, 156 dihaploid B- to D-clones were assessed in the field in year 1999, and still 120 in 2000, 41 were crossed. 54 dihaploid A-clones with late blight resistance were tested in 2002, 54 with expected suitability for chips, 117 for French fries, 144 for table potato quality, 73 for starch and 46 for resistance to *G. pallida*. At the same time 18 dihaploid B- to D-clones continued to be assessed for late blight resistance, 27 for crisps, 44 for French fries, 50 for table quality, 11 for starch and four for *G. pallida*. 120 cross combinations were planned on diploid level for late blight resistance that year.

Some of available *dihaploid* pre-breeding clones resistant to *P. infestans* (fig. 130) were distinguished by good quality traits as suitability for French fries (fig. 131), starch or table potato (table 52). Figure 132 and 133 present early maturing (score 6) clones with high foliage blight resistance, which allowed only slight attack and nearly undisturbed to grow ripe under high infection pressure. However, in figure 132 no any quality trait is sufficiently expressed. Several

clones in table 52 are described with foliage or tuber blight resistance below score six. These are excluded from backcrossing and would be used for inter-crosses, but all clones of table 52 are male sterile. Therefore use of advantage to breed on diploid level (Howard 1970, Ortiz & Peloquin 1994) can not effectively be realised up till now by crossing late blight resistant x late blight resistant. Some highly blight-resistant dihaploids do not flower. Early to second-late maturity is present on the quantitative blight resistant clones (table 52), a fact, which is usually considered to be too difficult (Allefs et al. 2005).

Table 52 Flowering dihaploid late blight-resistant clones of ZL Gross Luesewitz.

BAZ-GL-	Foliage blight	Tuber resistance	French fries	Crisps	Starch content	Culinary index	Shape along	Maturity
86.082.01	4.8	7.0	6.0	5.3	21.6	902	4.0	4.9
89.023.66	7.5	5.0	5.0	4.0	18.0	748	5.5	4.8
93.6997.07	8.7	8.1	7.0	5.8	19.3	861	4.7	4.8
94.7171.62	7.0	5.8	5.0	4.8	18.3	737	5.0	3.0
97.0094.01	5.3	6.3	3.0	2.8	14.0	928	4.4	4.4
97.7006.01	8.9	7.2	5.0	6.0	13.8	687	4.3	3.6
99.8142.01	5.7	8.5	5.5	4.5	13.0	769	5.8	6.6
99.8205.01	6.0	8.1	4.5	3.5	12.7	858	5.5	5.3
00.1029.11	6.3	7.1	6.0	5.0	16.7	813	5.0	4.4
00.1070.02	5.1	5.8	6.8	5.3	16.4	660	5.0	3.8
01.1505.02	5.2	6.7	-	4.7	16.8	624	3.0	3.7
01.1536.07	7.9	8.0	-	3.5	15.5	805	4.0	2.9
01.1537.02	8.8	9.0	5.0	4.0	18.6	616	5.0	5.6

Score 9: best expression of a trait. Tuber shape alongside: 3: round, 5: oval, 7: long, 9: kidney-shaped. Maturity: 3: second late, 5: second early, 7: early, 9: very early.

Because of limited manpower the part of dihaploid clones was reduced to 19% of the grown pre-breeding material in 2006. Results of the breeding stage 2006 are given in detail in chapter 7. For some little time an opportunity is known to overcome the fertility problems by switching from out-breeding to selfing of dihaploids. Precondition is crossing with a homozygous progenitor of the *Sli* gene, which inhibits gametophytic self-incompatibility and gives self-compatible offspring. Selfing and crossing then open quite new possibilities of breeding on diploid level up to hybrid breeding programmes (Lindhout et al. 2011, Meijer et al. 2011). Together with results of Yermishin et al. (2002, 2011) breeding on diploid level could have quite good chances now.

About 80% of the pre-breeding potato clones at ZL are tetraploid. In 2005 following tetraploid and diploid clone numbers were grown: 7,500 seedlings, 1,720 single hill-clones, 964 A-clones, 101 B-clones, 94 C-clones, 66 D-clones, 191 elder clones. About 70% belonged in the late blight programmes, 20% for processing, table quality or starch, 10% to produce cross parents with highest resistance to *G. pallida* or viruses.

6.5.6. Crossing and protoplast fusion

In 2001-2005 seeds of 274-642 cross combinations were sown yearly (table 53, last line). Depending from quality trait expression in the wild donor clones of blight resistance several following generations possess insufficient quality level as preliminary breeding stages on the way to the aim. Such crosses were not integrated within counting of promising combinations and not within mentioned utilization groups in table 53. The part of promising combinations increased; the percentage is related over all listed purposes. For instance, in 2002 120 cross combinations were applied to wild clones or BC1-BC3. Most combinations were produced for table potato quality as the most difficult part. The small part for starch production is combined more and more with resistance to *G. pallida* and as generally with second early maturity.

Protoplast fusion earlier was used in large scale in addition to crossing, mainly for progress in processing by colleagues K. Sonntag, H. Tiemann and R. Thieme (Thieme et al. 2004). For instance in 1997 376 hybrids of 53 combinations were produced, from which 104 clones were grown in the field in 1998 together with 52 elder ones to select tetraploid cross parents suitable for French fries or crisps. Inbreeding depression hampered selection of suitable tetraploids mainly concerning tuber size and tuber form from fusion in contrast to crosses with Canadian dihaploids.

Table 53 Number of cross combinations in five years: overall number includes F1 to BC3 and BC4-5 to produce suitable cross parents for own programmes (these are only in last line considered), and the part of BC4-5 from which desired trait combination on high level is expected (second line), in groups of different trait combinations and ploidy level.

		Percentage of cross combinations in the year				
Breeding objective	Ploidy	2001	2002	2003	2004	2005
Promising combinations (%)	-	49	70	85	77	88
Blight resistance/Table quality	4x	20	34	46	45	44
	2x	1	1	4	4	8
Blight resistance/Processing	4x	5	8	12	15	15
	2x	1	1	5	4	4
Blight resist./Starch production	4x	8	12	9	4	7
	2x	1	0	0	1	1
Blight/Starch /*G. pallida* resist.	4x	8	9	4	1	6
	2x	0	1	0	0	0
G. pallida resistance/Starch	4x	1	1	3	1	1
	2x	2	0	2	0	0
G. pallida resistance/Processing	4x	0	1	0	1	4
	2x	2	1	0	1	2
G. pallida resistance/Table quality	4x	0	1	0	0	5
	2x	0	0	0	0	1
Cross combinations, number overall		519	642	381	544	274

Dihaploid clones were grown in the breeding garden of ZL Gross Luesewitz in 1998 as follows:

3,700 single hills, 203 A-clones, 208 B-clones and elder ones, mainly suitable for table or processing purposes. In 1999 45% of the tested dihaploids showed low discolouration (score 7-9) after processing which corresponds with industrial producers requirements.

Last 10 years protoplast fusion was used to combine best dihaploid late blight resistant dihaploids (partly without flowering) with such suitable for processing or/and resistance to *G. pallida*. Only 16 of 44 desired combinations succeeded and 10% were hybrids; interspecific backcross hybrids proved to be more difficult to regenerate than *tbr*. 56 of 88 combinations failed in another experiment because of insufficient somatic combining ability. It means that this biotechnological method only partly can realize determined combinations, but it is a helpful tool.

6.5.7. Combining of blight resistance with insensitiveness to mechanical damage and resistance to *Erwinia* sp. and *Fusarium* sp.

Because of the importance of mechanical damage of tubers for entrance of *Erwinia* sp., *P. infestans* and *Fusarium* sp. into tuber tissue susceptibility to damage was generally tested by means of pendulum device according to Gall et al. (1989) since 1973. About 20% of breeding material was rejected due to susceptibility. Additionally susceptibility to *Erwinia* sp. and *Fusarium* sp. was assessed since the end of 1970ies in the department of pathology of the IK Gross Luesewitz on pre-breeding material for late blight resistance too (Darsow 1998b). In the 1980ies was found that our late blight resistant pre-breeding material had in majority a higher resistance level than variety level to soft rot caused by *Erwinia carotovora* ssp. *atroseptica* (*Eca*, Darsow & Roeber 1998, Wegener 2002).

Table 54 shows that variance of clones was half that of years and similarly of interaction year x clone. The genetic variance had a part of 19 % of total variance of soft rot – not hopeful conditions for resistance breeding. Calculation with two standard cultivars over three years and four replications resulted in a lowest significant difference of 0.6 scores or 10% rotting tubers.

Table 54 Analysis of variances in assessment of 32 dihaploid clones for resistance to soft rot (% of rotten tissue) caused by *Erwinia carotovora* ssp. *atroseptica* in two years by two laboratories (BBA Braunschweig, BAZ Aschersleben).

Sources of variation	Sums of squares	Degrees of freedom	Mean squares[1]	Variance ratios	F-probabilities
Total	113,814.082	127	896.174	-	-
Year	2,851.541	1	2,851.541[+]	6.01	3.99
Clone	44,428.758	31	1,433.186[+]	3.02	1.63
Laboratory	687.758	1	687.758	1.45	3.99
Year x Clone	35,947.585	31	1,159.600[+]	2.55	1.84
Year x Laboratory	434.277	1	434.277	0.96	2.50
Clone x Laboratory	15,375.217	31	495.980	1.09	1.84
Residual	14,089.288	31	454.493	-	-

[1)]: significant effect[+] at α=0.05

Better preconditions for breeding progress were connected with a method which considers two additional factors, inoculation with *Fusarium* and susceptibility to mechanical damage. Combined assessment of resistance of tubers against *Erwinia carotovora* ssp. *atroseptica* (10^4 cells/ml) and *Fusarium sulphureum* (10^4 conidia/ml) was carried out by dipping of a sample of 20 tubers per clone in four litre suspension after damaging it 30 seconds by falling in a drum-type sieve before inoculation (Darsow & Roeber 1998). 14-33% significant clonal differences enabled negative selection to improve main components involved in the complex of tuber rots in con-

ditions of crude technique for harvest and storage. Summarised results are shown in table 55.

Table 55 Part of rotting tubers (% with < score 8 in 1-9 scale of increasing resistance) in combined test for resistance to *Erwinia*/*Fusarium* with 20 tubers per clone after 30 seconds falling in a drum-type sieve before inoculation.

		Percent of rotten tubers			
Material	Years of assessment	min.	max.	mean	Percent of significant clonal differences
12 varieties	1985-1987	20	100	74.7	25
10 varieties	1986-1988	30	100	72.7	33
41 pre-breeding clones	1985-1987	5	100	53.4	28
19 pre-breeding clones	1986-1988	0	095	37.0	14
19 pre-breeding clones	1987-1989	0	095	41.2	16
13 pre-breeding clones	1988-1990	0	090	29.4	26

Standard varieties showed a highly constant infection level. The resistance behaviour to *Erwinia* sp. and *Fusarium* sp. could be explained to 24% by pendulum-results. Beyond it, we experimented with a combined *Erwinia/Phytophthora* resistance test on tubers. Slow breeding progress was stated; however, reduced manpower did not enable to continue working on this complex. That time we did not select for smooth skin. There was the impression that rough skin made more robust to the assessed complex of traits.

6.6. Pre-breeding as bridge between gene banks (and research) and variety breeding is neglected in most countries

The main reason for insufficient breeding progress in difficult polygenic determined traits of potato is generally neglecting of pre-breeding as provision for long-term solutions, providence for generation of our children (see chapter 3.3.). Preparing of utilization of quantitative resistance against late blight at Gross Luesewitz is an example for the importance of established pre-breeding between gene bank and cultivar breeding. The fact that pre-breeding is lost (for instance at MPI Cologne-Vogelsang) or difficult to establish (USA, Pavek & Corsini 2001) is due to low adaptability to established structures of applied science (see chapter 3.3. and 10.3.). Pre-breeding requires much higher manpower than research and can not contribute yearly with new attractive results; its precondition for success is thinking in small long-term steps and withstanding interpretation of short-term tendencies. The lack of a frame that enabled purposeful complex long-term public pre-breeding aimed at needs of (private) cultivar breeding causes missing progress concerning specific tasks in permanent social interest as increasing quantitative late blight resistance. On the other hand variety breeding can not take over this task because of the cost/profit difference of decades, different routine and different specific know-how. The application of pre-breeding for quantitative late blight resistance is accompanied with the public interest to more consequent pollution control and is therefore beyond all doubt a public task. Such pre-breeding usually will be applied for enhancement of other traits too, at the beginning partly separate, later on overlapping.

7. State of systematic pre-breeding for combining quantitative late blight resistance on foliage and tubers with quality traits, represented by results in 2006.

7.1. Assessment of traits and presentation of results

Each clone passes through three years assessment of 68 traits as B-, C- and D-clone in third to fifth year of growing in the field (examination of performance, table 40, 42). Usually up to 160 clones are yearly new integrated within examination of performance; their number nearly halves yearly. Between 379 clones and cultivars in 2006 248 own tetraploid and 61 dihaploid clones were grown with breeding aim resistance to *P. infestans*. Among the tetraploids 133 clones belonged to combination resistance to *P. infestans*/table potato, 44 to resistance to *P. infestans*/processing, and 40 to resistance to *P. infestans*/starch. A part of resistant clones can not be related to any utilization. Results of the whole material grown in 2006 are shown before selection between harvest and next planting in 2007; results of standard cultivars are given for comparison. So the information is not presentation of selected best results and is more than presentation of only results of a single year. 68 traits are presented as frequency distribution in three groups: **1**. tetraploids with maturity very early to middle of second early (ese), **2**. later part of second early to late tetraploids (sla), **3**. dihaploids. Parting of tetraploids inside of the second early group had practical reason as grouping for the harvest date. Only few clones of BC2 or BC3 were included. Single clones are partly presented on figures and were shortly characterized after its clone number or in tables in chapter 6.

The applied methods and remarks to the traits and its inheritance in chapter 4 should be considered for evaluation of the breeding state.

7.2. Results of 21 traits on haulm in pre-breeding material 2006

Among traits of haulm maturity and foliage blight resistance are of highest interest and are therefore put in front. Maturity of 248 tetraploid and 61 dihaploid clones resistant to *P. infestans* was assessed with three methods in parallel: 1. scoring of progress of yellowing of haulm, 2. number of days from date of planting to date of death of haulm, 3. number of days from date of emergence to date of death of haulm. The frequency distribution of three groups in classes of maturity according to yellowing of haulm is nearly randomly (fig. 134). Main value of all tetraploid clones was 5.2, exactly second early on the scale 9-1. About 6% of blight resistant clones were even early to very early (score 8), 14% passed for early (score 7), 20% for early to second early (score 6) and 31% for second early (score 5), 19% matured second early to second late (score 4), and only 10% second late. Very late was only one dihaploid clone, apart from that very late material was eliminated in BC3 and BC4 by selection considering stolon length and lateness as seedling or in first field year. Included standard cultivars grown for comparison get in average of three replications the following scores: Adretta 6.7; Karlena 6.5; Marabel 7.8; Agria 4.5; Jelly 3.4; Steffi 3.8; Kuras 2.9. These data show that the main argument against use of polygenic blight resistance for long day conditions in literature, highly negative correlation between resistance of foliage and earliness (Visker 2005, Allefs et al. 2005), is without object in our pre-breeding at ZL Gross Luesewitz (see fig. 29, 30, 96). This fact is sure, although is admitted that conditions during vegetation period 2006 supported earlier maturation. However, deviations of more than 0.7 scores to maturity of other years occurred on lesser than 10% of clones up to 1.6 scores, mainly in case of fusionates, which can be estimated only very roughly in first field growing. Clones of crosses with wild species and its BC1 are very late in our conditions too, but are grown outside of this frame of examination of performance (see table 42).

Results of the second method to assess maturity according to number of days between date of planting and date of death of haulm give an oblique distribution (fig. 135). As well for tetraploids as for dihaploids on average 121 days were calculated. Cultivar Marabel was dead after 105 days, Karlena after 107, Adretta after 112, Agria after 115, Steffi after 132, Jelly after 139, and Kuras after 163 days. One clone was later than Kuras.

Assessing maturity by number of days from date of emergence to date of death of haulm resulted in 93 days on average of tetraploid material and 90 days on dihaploids (fig. 136). Marabel had 76 days of vegetation, Karlena 82, Adretta 91, Agria 87, Steffi 101, Jelly 109, Kuras 131 days. Only 3% of tetraploid clones corresponded to Kuras, no one was later. Both 'objective' methods using number of days are more time-consuming. They correlated with each other on tetraploid material with r = 0.51 and on dihaploids with r = 0.96. To method 1 (scoring) r = -0.43 respectively r = -0.68 were calculated for tetraploids und r = -0.75 and r = -0.76 in case of dihaploids. Because counting of days included all other reasons of haulm death, we prefer repeated assessment of yellowing; an experienced person can largely correct other influences on dying of haulm in that stage.

Resistance of foliage to *P. infestans* in field assessment: In opposite to most other experiments with late blight in Central Europe we obtained well suitable results even in 2006. In the early group (ese) 120 own pre-breeding clones were tested (see fig. 21, 22), in the second late group of tetraploids (sla) 113 clones, additional 59 own dihaploid clones. The whole range from very susceptible (score 1) to highly resistant (score 9) was established (fig. 137). Nearly 31% of the early group, 44% of second late group, and 66% of dihaploids were thrown away according to these results before next planting. In case of C- and D-clones results of 2006 or 2005 and 2004, respectively, have been considered for selection. Standard cultivars obtained in average of three replications the following scores: Erstling 1.9, Gloria 2.3, Karlena 2.1, Marabel 3.4, Adretta 2.4, Tomensa 2.7, Alpha 2.0, Bintje 1.5, and Kuras 7.4. The relation to standards shows the potential of clones from ZL conceivable in integrated plant protection. In the course of vegetation several other traits were estimated. Frequency distribution to scores 9-1 of 125 early to second early blight resistant tetraploids (4x ese), of 123 second early to late clones (4x sla), and 61 dihaploid clones is shown in table 56.

Table 56 Percentage of clones (%) of ILK Gross Luesewitz in score-classes of haulm traits.

Material	Score								
	9	8	7	6	5	4	3	2	1
	Uniformity of emergence (9 = very uniformly)								
P. i.-resistance, 4x ese	1	13	28	31	17	8	2	0	0
P. i.-resistance, 4x sla	0	8	23	35	25	8	1	0	0
P. l.-resistance, 2x	0	19	36	20	14	8	3	0	0
	Juvenile haulm growing (9 = very speedy)								
P. i.-resistance, 4x ese	8	15	23	27	21	5	1	0	0
P. i.-resistance, 4x sla	0	6	27	30	32	5	0	0	0
P. l.-resistance, 2x	0	0	4	15	37	37	7	0	0
	Haulm mass (9 = very bulky)								
P. i.-resistance, 4x ese	0	2	16	45	30	7	0	0	0
P. i.-resistance, 4x sla	0	3	19	57	20	1	0	0	0
P. i.-resistance, 2x	0	0	10	35	36	17	2	0	0

Material	Score								
	9	8	7	6	5	4	3	2	1
	Facility visually to diagnose virus infections (9 = very easy)								
P. i.-resistance, 4x ese	0	1	10	30	36	22	1	0	0
P. i.-resistance, 4x sla	0	0	13	34	37	15	1	0	0
P. I.-resistance, 2x	0	0	5	14	54	27	0	0	0
	Intensity of flowering (9 = very reach)								
P. i.-resistance, 4x ese	0	2	10	17	28	39	12	2	0
P. i.-resistance, 4x sla	0	0	3	20	33	30	12	2	0
P. I.-resistance, 2x	0	2	14	24	36	14	8	0	2
	Spontaneous setting of berries in field (9 = a great many)								
P. i.-resistance, 4x ese	0	0	6	6	9	10	22	15	32
P. i.-resistance, 4x sla	1	4	2	4	8	17	20	15	29
P. I.-resistance, 2x	0	0	0	2	0	0	5	4	89
	Stability of haulm in field (9 = very stable)								
P. i.-resistance, 4x ese	0	1	29	43	18	9	0	0	0
P. i.-resistance, 4x sla	0	2	32	48	16	2	0	0	0
P. I.-resistance, 2x	0	2	13	42	10	25	8	0	0
	Plant height (9 = very highly)								
P. i.-resistance, 4x ese	0	3	17	40	30	10	0	0	0
P. i.-resistance, 4x sla	0	2	34	52	11	1	0	0	0
P. i.-resistance, 2x	0	0	14	33	41	12	0	0	0

Standard cultivars were scored for uniformity of emergence from 4.7 to 7.5, so blight resistant clones showed no disadvantage in comparison. Juvenile haulm growing of standards was scored with Karlena 6.8, Marabel 5.2, Adretta 7.8, Agria 6.3, Jelly 5.8, and Steffi 4.5. Tetraploid pre-breeding material has the same level. Dihaploids develop slower, however a good result is attained in international comparison. Very bulky haulm mass with score 9 is not desired on yield-physiological and epidemiological reason (microclimate, duration of high relative humidity and of free water on leaf surface, respiration rate, light interception). Score six coincides with the breeding aim for conventional growing, seven for ecological farming. Standard cultivars were estimated 4.7-6.0. The level of dihaploids is agreeable.

Facility visually to diagnose virus infections represents an important trait as long as visual selection of virus infected plants in the field in seed potato production is usually. Scores 4-1 makes recognition of symptoms more difficult, score six and better considerable improve reliability of recognition. Standards were scored 4.0-6.3. Improved level of dihaploids is particularly emphasized compared to past.

Fertility of pre-breeding material enabled generally its use for crossing. Therefore poor flowering clones with flowering intensity 2.0 or 3.0 are kept only exceptionally, without flowering threw away. Standards flowered with score 2.3-5.0. In particular for breeding on diploid level, the high part of missing bloom and missing spontaneous setting of berries in the field mean a hindrance as a sign of missing male fertility. If berries set according score 4 or better, male fertility may be expected. More than a third of our tetraploid clones are male fertile and suitable as pollinator, whilst only one dihaploid clone (table 56).

High stability of haulm in the field results in better utilisation of sun light, less contact with soil surface, shorter duration of free water on leaf surface. With regard to change of climate it will gain in importance. This trait is staggered to estimate depending from maturity. Our data correlated with maturity only modest, r = -0.39. Mean value of tetraploid material amount to score 6.0, which means between middle and good.

Very high plant height with score 9 is not desired, score 7 required at minimum stability of haulm seven to withstand strong wind and not premature to lie down. Both, in 4x- and in 2x-material a level near cultivars is reached. Plant high of standards was scored 4.0-5.8.

Infestation with *Alternaria* sp. occurred more frequently in 2006 because of warm, dry summer. Dew, fog and high temperature promoted infection. Often infection with *Botrytis cinerea* followed during progressed maturation. Because of frequently combined occurrence and merging of symptoms into each other both diseases were estimated together (fig. 138). The second late group was more intensive seized with it (fig. 139). Nevertheless, there was no correlation to maturity (r = < 0.1). Scores 2-9 were given in all three groups of pre-breeding material. Clones with score two and three were later eliminated. Standard cultivars were estimated as follows: Karlena 4.3, Marabel 6.2, Adretta 5.7, Agria 2.3, Jelly 4.5, Steffi 5.2, and Kuras 5.5 in the scale 9-1, in which 9 means free of symptoms. Higher susceptibility of *S. demissum* to *Alternaria sp*. is mentioned too by Rudorf and Schaper (1951).

Leave type (score 1) und stem type (score 5) describe the range of growing habit. Both do not coincide with breeding objective, but score 2-3 is desired in earlier and 2.5-4 in later material. Utilization of sun light, weed cover and haulm/tuber-relation are connected with it. Standards were scored 2.2-3.0. Also concerning this trait, clones of ZL correspond with breeding objective (table 57).

Table 57 Percentage of pre-breeding clones (%) in score-classes of growing habit.

Material	Score								
	1	1.5	2	2.5	3	3.5	4	4.5	5
P. i.-resistance, 4x ese	0	4	25	27	31	8	5	0	0
P. i.-resistance, 4x sla	0	0	11	28	44	11	4	2	0
P. i.-resistance, 2x	0	0	7	18	50	12	13	0	0

Number of main stems belongs to determinants influencing size and number of tubers and yield (table 58). Its clone-specific expression is influenced by conditions of storage and by pre-sprouting. Since more than seven or only 1-2 main stems are connected with too small or very big tubers, respectively, such clones are only of interest for special purpose. Three to six stems correspond to most purposes. The distribution in our material is represented in table 58. Cultivar Agria developed 1.9 stems; other standards had 3.0-4.3 stems per plant. Clones with only one ore more than nine stems were threw away.

Table 58 Percentage of pre-breeding clones (%) with following number of main stems.

Number of stems	≥ 9	8	7	6	5	4	3	2	1
P. i.-resistance, 4x ese	10	5	6	6	16	24	25	7	1
P. i.-resistance, 4x sla	1	1	3	11	17	25	31	10	1
P. i.-resistance, 2x	5	11	14	18	30	16	3	3	0

Lasting drought in July and August 2006 caused a wide range of flaccidity in early afternoon, which was scored as measure of drought tolerance. Scores 8-3 or 7-2 were given in the three

groups (fig. 140). Karlena got 6.0, Marabel 4.2, Adretta 4.0, Agria 5.0, Jelly 6.0, and Kuras 7.0. Maturity correlated with drought tolerance with r = 0.26 or r = 0.38 in case of tetraploid material, with r = 0.70 on dihaploid clones, at which early maturity was connected with lesser tolerance. Correction by calculation of regression would mainly improve the estimation of dihaploid clones. Scores between two and eight were found on early maturing tetraploid clones (maturity 7), which shows a high diversity and basis for selection. 28 drought-tolerant, blight-resistant clones were counted in 2006. Additionally six elder drought-tolerant clones were selected in a year with extreme aridity at Aschersleben. However, systematic breeding for drought tolerance needs a suitable method or location for yearly reliable assessment. Presented results show potential of combining blight resistance with drought tolerance and other traits in pre-breeding material of ZL.

The colour of flowers in progressed pre-breeding material of ZL has a broad range, although white dominates (table 59).

Table 59 Percentage of pre-breeding clones (%) with different flower colour.

Colour	white	very light violet	light violet	violet	light blue	blue violet	blue	rose violet	rose
P. i.-resistance, 4x ese	62	4	10	9	4	5	3	1	2
P. i.-resistance, 4x sla	55	6	17	5	5	8	1	1	2
P. i.-resistance, 2x	54	0	0	24	8	6	2	0	6

Attack with virus diseases partly dramatically affects vitality of potato plants, especially of wild species and first line caused by PVY und PLRV. Virus infections decrease efficiency of crossing, influence expression of some other traits; they cause extended growth area in breeding garden and premature loss of valuable clones. Data of seed production of 316 pre-breeding clones, grown only continuously *in vivo* without recourse to virus-free plants *in vitro*, showed after a season with an aphid population higher than usually over longer time a low initial infection level for 2007 (table 60). All clones with >20% PVY, PLRV, PVA or PVM were eliminated. However, in case of progressed pre-breeding material present level of virus resistance enabled in our breeding garden to get healthy clones from such with 2/10 PVY- or up to 5/10 PLRV-attacked plants by early selection. In contrast to that, virus infections are the main reason to lose wild clones as source of resistance or its progeny. PVY is most important. Infections with PLRV increase since about 2001. PVM rarely occurs, PVA similarly. Standard cultivars were infected with 50-100% PVS at the same conditions, Agria additionally with 17% PVY, Kuras with 22% PVA. The results show success of combination breeding to reduce susceptibility to PVY of donors of resistance to *P. infestans* started from.

Table 60 Percentage of clones (%) from ZL Gross Luesewitz in classes of virus infections after harvest 2006.

		Occurrence of virus diseases among 10 plants tested with ELISA								
		≤ 20%	>20%	≤ 20%	>20%	10-30	31-80	>80%	10-50%	
Material	Healthy	PVY	PVY	PLRV	PLRV	PVS	PVS	PVS	PVM	PVA
P. i.-resistance, 4x ese	30	8	0	4	5	27	21	22	0	4
P. i.-resistance, 4x sla	27	6	2	6	1	20	27	25	5	6
P. i.-resistance, 2x	41	5	4	6	14	24	18	15	0	6

Cultivated cross parents with high complex virus resistance are a fundamental precondition for efficient or really succeeding utilisation of wild species. ZL has clones, which for about 30 years grown in field are free of viruses or only invaded by PVS. These were preferred for crossing of wild species or first backcross.

7.3. Results of pre-breeding material for 17 tuber traits

Now tuber traits are considered, which are of similar interest for all aspects of exploitation as table potato, starch or processing products.

Tuber blight resistance of freshly harvested, whole tubers: Defence of skin is in our growing conditions more important than defence of tuber medulla. 124 very early to second early tetraploid clones (ese), 125 second early to late (sla) tetraploid ones and 57 dihaploids were assessed (fig. 141). The higher part of highly resistant clones was supported by environmental conditions of 2006. The whole range from score nine to one occurred. Clones with tuber blight resistance below 4.5 will be thrown away. Standards had following results: Adretta 2.5, Karlena 5.8, Marabel 3.3, Jelly 4.0, and Steffi 6.4. Compared with these, tetraploid clones of ZL support foliage blight resistance by a high level of resistance on tubers. Resistance of tested dihaploids in 2006 was mainly insufficiently.

Tuber blight resistance in tuber slice test: A third to the half of tetraploid clones showed increased to nearly very well resistance (fig. 142), whilst Adretta got score 3.3, Karlena 3.6, Marabel 3.4, Agria 3.6, Jelly 3.9 and Steffi 5.8. Combination of resistance of tuber pith and skin is considered as epidemiological valuable supplementation of foliage blight resistance (Darsow 2004/5 a).

As well internal rust spot, hollow heart as cracking of tubers occurred in 2006 lesser than usual (table 61). Standards did not show these defects in 2006. The few clones with more than four percent of these faults were intended to eliminate.

Table 61 Percentage of clones (%) with external and internal defects of tubers.

Part (%) of defect tubers in crop	0	1-4	5-9	10-14	15-19	20-24	>24
	Part of clones with cracked tubers						
P. i.-resistance, 4x early to second early	93	4	2	1	0	0	0
P. i.-resistance, 4x second early to late	96	3	1	0	0	0	0
P. i.-resistance, 2x	97	3	0	0	0	0	0
	Part of clones with hollow heart-tubers						
P. i.-resistance, 4x early to second early	92	4	2	2	0	0	0
P. i.-resistance, 4x second early to late	89	5	2	4	0	0	0
P. i.-resistance, 2x	100	0	0	0	0	0	0
	Part of clones with tubers with internal rust spot						
P. i.-resistance, 4x early to second early	94	0	0	6	0	2	0
P. i.-resistance, 4x second early to late	96	0	0	8	0	2	0
P. i.-resistance, 2x	97	0	0	0	0	0	0

Lasting drought determined main part of growing period 2006 and led to yield in breeding garden below 50% of the normal yield. About 58% of tetraploid resistant clones produced lesser than 600g per plant. 72% of dihaploid clones yielded lesser than 300g per plant (fig. 143).

Table 62 Number and part of clones (%) of ZL Gross Luesewitz in score-classes of traits.

	Number	Score								
Material	Clones	9	8	7	6	5	4	3	2	1
		General impression of tubers (9 = very well)								
P. i.-resistance, 4x ese	79	0	5	68	20	7	0	0	0	0
P. i.-resistance, 4x sla	76	0	1	48	43	8	0	0	0	0
P. i.-resistance, 2x	31	0	0	23	33	34	10	0	0	0
		Uniformity of tuber size (9 = very uniformly)								
P. i.-resistance, 4x ese	79	0	1	6	14	19	46	14	0	0
P. i.-resistance, 4x sla	76	0	2	15	24	23	24	12	0	0
P. i.-resistance, 2x	30	0	0	0	0	0	40	60	0	0
		Tuber size (9 = very large)								
P. i.-resistance, 4x ese	79	1	0	12	39	36	12	0	0	0
P. i.-resistance, 4x sla	76	0	4	20	38	28	10	0	0	0
P. i.-resistance, 2x	31	0	0	0	0	13	70	17	0	0
		Beauty of shape of tubers (9 = very beautifully)								
P. i.-resistance, 4x ese	79	1	20	39	36	4	0	0	0	0
P. i.-resistance, 4x sla	76	0	5	47	43	5	0	0	0	0
P. i.-resistance, 2x	31	0	10	26	29	29	6	0	0	0
		Shape in longitudinal direction (9 = kidney-shaped)								
P. i.-resistance, 4x ese	79	0	0	0	19	46	18	17	0	0
P. i.-resistance, 4x sla	76	0	0	2	19	38	27	14	0	0
P. i.-resistance, 2x	31	0	0	0	13	32	23	12	0	0
		Shape crossways (9 = round, full)								
P. i.-resistance, 4x ese	79	0	28	67	4	1	0	0	0	0
P. i.-resistance, 4x sla	76	0	20	71	9	0	0	0	0	0
P. i.-resistance, 2x	31	0	26	71	3	0	0	0	0	0
		Defect of shape (9 = no defect)								
P. i.-resistance, 4x ese	80	1	18	43	32	6	0	0	0	0
P. i.-resistance, 4x sla	74	0	9	30	45	15	1	0	0	0
P. i.-resistance, 2x	31	0	3	42	16	29	10	0	0	0
		Eye depth (9 = very shallow)								
P. i.-resistance, 4x ese	80	0	16	41	24	18	1	0	0	0
P. i.-resistance, 4x sla	76	0	3	32	31	26	8	0	0	0
P. i.-resistance, 2x	31	0	16	33	19	22	10	0	0	0
		Hilum (9 = not detectable)								
P. i.-resistance, 4x ese	80	0	9	31	46	14	0	0	0	0
P. i.-resistance, 4x sla	76	0	1	24	42	30	3	0	0	0
P. i.-resistance, 2x	31	0	3	16	29	33	16	3	0	0
		Dormancy (9 = very long, deep)								
P. i.-resistance, 4x ese	80	0	0	12	29	26	23	9	1	0
P. i.-resistance, 4x sla	76	0	1	13	32	38	13	3	0	0
P. i.-resistance, 2x	31	0	3	3	7	26	35	19	7	0
		Resistance to *Erwinia*-soft rot (9 = highly resistant)								
P. i.-resistance, 4x ese	29	52	17	10	7	0	0	7	0	7
P. i.-resistance, 4x sla	24	62	12	9	6	9	2	0	0	0

However, decisive is comparison with standards: Karlena yielded 609g, Marabel 610g, Agria 665g, Jelly 710g, and Kuras 949g. Because 42% of tetraploid pre-breeding clones produced 600-1000g per plant, yield is near to cultivar level.

The number of tubers per plant ranged from 5 to 30, the frequency distribution of clones with ≤7 to ≥20 tubers is represented in figure 144. The second-late group set lesser tubers than the earlier one. Dihaploids showed strongest reduction of tuber number. Also standards did not develope usual numbers: Karlena 10 tubers, Marabel 9, Agria 6, Jelly 8, and Kuras 10. Nearly half the resistant clones had more than 10 tubers, which most remained smaller.

More than half the tetraploid clones came up tuber size of standards: Karlena 6.3, Marabel 6.7, Agria 7, Jelly 7.2 and Kuras 7.5 (table 62). Increase of tuber size goes on to be a task for table and processing purpose.

Two third of early and half of second late group showed good (score 7) or better general impression of tubers. Standards were estimated with: Karlena 6.0, Marabel 7.5, Agria 7.2, Jelly 8.0 and Kuras 5.5. The level of best cultivars was sporadically achieved. Uniformity of tuber size 6-7 was expressed on standards and 10-20% of tetraploid clones. Often part of small tubers was too high. Table 62 includes all directions of utilization before selection for growing 2007.

Beauty of shape of tubers is profitable by a technical advantage and additional entices consumers. Standards were estimated with: Karlena 5.8, Marabel 7.8, Agria 7.0, Jelly 8.2, and Kuras 5.0. About 60% of the earlier tetraploid group and half the later one were scored ≥7 and show cultivar level. Dihaploids obtained this level with one third (table 62).

Shape in longitudinal direction with score 6-7 is desired for French fries production, a fifth of tetraploid material corresponds with it in 2006. Oval shape dominates. Karlena got 4.0, Marabel 6.0, Agria 6.0, Jelly 5.7, and Kuras 4.0. Tubers with ideal shape crossways are full and round in cross-sectional view. Our pre-breeding material approached to breeding objective. Standard cultivars were scored like this: Karlena 6.8, Marabel 7.3, Agria 7.0, Jelly 7.3, and Kuras 7.0.

Assessment of shape defects rated mainly score seven and six, whilst Karlena had 5.5, Marabel 7.8, Agria 7.5, Jelly 8.0, Kuras 5.0 (table 62). Clones of ZL expressed this trait near cultivar level. Eye depth of earlier tetraploid group (81% ≥ 6) was more flat than of later group (66% ≥6). Karlena got 5.2, Marabel 6.7, Agria 7.0, Jelly 7.3, and Kuras 5.5. So, eye depth belongs to the many traits, which do not impede using of inheritors for quantitative blight resistance.

Inconspicuous forming of tuber hilum reduces as well injury and infections as adherent soil and wastage due to peeling. Since 86% or 67%, respectively, of tetraploid clones were scored ≥6; its use in cultivar breeding should cause no problems concerning this trait. Standard Karlena had score 5.0, Marabel 7.0, Agria 7.0, Jelly 7.2, and Kuras 4.0 (table 62). For starch production lesser scores of both last traits are sufficiently.

Deep, long lasting dormancy decreases loss during storage, saves de-sprouting and facilitates storing out. Mainly in working with dihaploids one can learn that dormancy is complex inherited. New literature underlines that (van Eck 2007). Deep dormancy is desired, but usually connected with delayed emergence. 67% of earlier or 84% of later tetraploid clones were characterized by middle to deep dormancy. In comparison to these Karlena was scored 4.3, Marabel 4.7, Agria 6.3, Jelly 6.0, and Kuras 4.0 (table 62). On tetraploid level dormancy of pre-breeding material coincides with cultivar level. Dihaploids require more breeding effort in this trait.

For a long time is known that our blight-resistant pre-breeding material possesses better quantitative *Erwinia-soft* rot resistance than cultivars (Darsow 1998b). However, even too high score level of standards enabled hardly selection in 2006/2007: Karlena 8.1, Leyla 4.0, Marabel 7.3, 9.0 for Steffi and Kuras (table 62).

7.4. Results in combining of resistance to *P. infestans* and suitability for processing

Results of assessment of processing traits of pre-breeding material in 2006/2007 are given in table 63 for earlier and later tetraploid group and dihaploids.

Table 63 Number of B- to D-clones, resistant to *P. infestans*, and its part (%) in score-classes of discolouration after baking to French fries or crisps 2006.

	Number	Score of colour								
Material	Clones	9	8	7	6	5	4	3	2	1
		Colour of French fries (9 = bright golden)								
P. i.-resistance, 4x ese	61	0	6	15	28	26	23	2	0	0
P. i.-resistance, 4x sla	54	2	11	17	24	24	18	4	0	0
P. i.-resistance, 2x	12	0	17	25	25	25	8	0	0	0
		Colour of crisps (9 = shining clear)								
P. i.-resistance, 4x ese	78	0	0	0	8	24	37	12	13	6
P. i.-resistance, 4x sla	74	0	0	0	3	16	37	20	19	5
P. i.-resistance, 2x	31	0	0	0	16	26	55	3	0	0

Clones with score seven suit for French fries (fig. 145), however, combined with large and long tubers without internal defects as internal rust spot and hollow heart. Good breeding progress is shown for combination of this utilization with blight resistance. One example is BAZ-GL-01.1293.01 P St Po Kr1 (see fig. 101). Systematic improvement requires continuation to combine good colour after frying with better tuber shape (longer) as visible on clone BAZ-GL-01.1272.03 P Sp (St) Po Ro1 with netted tuber skin, but only oval shape (fig. 146). Fry colour belongs according to Bradshaw (2007a) to the highly heritable traits. More suitable cross parents will make it more successfully to breed blight-resistant new cultivars for production of French fries in future. Combining with suitability for crisps is in our pre-breeding in its infancy. Clone BAZ-GL-00.1195.13 P St Ch is resistant to late blight and suitable for crisps (fig. 147).

7.5. Results in combining of resistance to *P. infestans* and high starch content

High starch content was introduced by cultivated cross parents. Therefore progress in little steps is expected and obtained (table 64). Partly resistance to *G. pallida* is expressed at the same time. Dihaploids usually have higher starch content due to smaller cell size.

Table 64 Number of B- to D-clones, resistant to *P. infestans* and its part (%) in classes of starch content in 2006.

	Number	Starch content (%)								
Material	Clones	≥25	24	23	22	21	20	19	17-18	≤16
P. i.-resistance, 4x ese	24	0	8	0	13	8	9	25	29	8
P. i.-resistance, 4x sla	33	0	6	6	7	2 7	27	21	6	0
P. i.-resistance, 2x	15	7	7	7	14	33	13	20	0	0

7.6. Results in combining of resistance to *P. infestans* and table potato quality

The most difficult combining of quantitative late blight resistance and good table potato quality is in sub-programme 'table potato/late blight' at ZL progressing. Discoloration after cooking to grey or dark is not desired. In assessment of 2006 cooked tubers were more discoloured than in other years; score four was most frequently expressed in all three groups (fig. 148). Good table potato cultivars got following scores: Marabel 5.8, Agria 5.2, Steffi 7.5, Jelly 5.3, Adretta 4.0, and Karlena 3.2. Only 8-13% of pre-breeding clones had scores six to eight, which indicates imperfect state of combination of resistance with this trait.

Index of table potato quality includes appearance after cooking, taste and discoloration after cooking; here the index is transformed into scores (fig. 149). Standard cultivars were assessed with score 4.7 for Karlena, 6.3 for Marabel, 6.0 for Agria, 6.7 for Jelly and 6.0 for Steffi. 10-30% of clones in the groups came up to that level. Results of additional traits are written in table 65.

Assessment of appearance after cooking of peeled tubers considered homogeneity of flesh colouration, glassiness of tissue, discolouration, change of structure and disintegration during cooking. 29-48% of clones were scored ≥4 (good, table 63). Standards obtained in average of three replications score 3.1 (Karlena), 4.4 (Marabel), 4.0 (Agria, Steffi) and 4.3 (Jelly).

Table 65 Part of pre-breeding clones (%) of sub-programme 'blight resistance/ table potato' in score-classes of culinary traits (score 1-5) in result of assessment 2006.

	Score								
Material	5	4.5	4	3.5	3	2.5	2	1.5	1
	Appearance after cooking (5 = very well)								
P. i.-resistance, 4x ese	0	10	19	35	24	10	2	0	0
P. i.-resistance, 4x sla	0	0	33	33	26	4	4	0	0
P. i.-resistance, 2x	0	0	48	28	14	5	0	0	0
	Consistency of cooked potatoes (5 = very firm)								
P. i.-resistance, 4x ese	0	0	4	24	29	38	5	0	0
P. i.-resistance, 4x sla	0	0	10	33	33	24	0	0	0
P. i.-resistance, 2x	0	0	0	10	29	61	0	0	0
	Disintegration during cooking (5 = not disintegrated)								
P. i.-resistance, 4x ese	4	15	17	28	20	11	2	0	0
P. i.-resistance, 4x sla	2	8	25	26	31	6	0	0	0
P. i.-resistance, 2x	14	28	19	10	24	5	0	0	0
	Mealiness (5 = not mealy)								
P. i.-resistance, 4x ese	0	0	4	25	26	39	4	2	0
P. i.-resistance, 4x sla	0	0	6	8	25	47	14	0	0
P. i.-resistance, 2x	0	5	19	33	14	19	10	0	0
	Taste (5 = very well)								
P. i.-resistance, 4x ese	0	2	2	35	29	28	4	0	0
P. i.-resistance, 4x sla	0	0	14	31	47	4	4	0	0
P. i.-resistance, 2x	0	0	5	15	33	33	14	0	0

Consistency of cooked tubers described solidity of cooked tubers as regularly firm (score 5) to slack outer part with very firm core (score 1). Nearly two third of clones cooked not compact (3) to a little firm (4), the rest more mellow (≤2.5. table 65). Dihaploids cooked mellower, standard cultivars as follows: Karlena 3.1, Marabel 4.0, Agria 3.8, Jelly 3.8, and Steffi 4.5. There is a difference in consistency to cultivar level, which is worked on.

Disintegration during cooking shows few clones with sleek surface (score 5); a third of tetraploid clones was a little cracked (score 4). A bit more than a third of tetraploids were too strong disintegrated after cooking (≤3). BAZ-GL-00.1185.01 P Sp is a clone with disintegration 2.7, consistency 3.3, mealiness 2.8 and taste 4 (fig. 150). Dihaploids corresponded better with the breeding aim. In comparison to that, Karlena was estimated 3.0, Marabel 4.6, Agria 4.0, Jelly 4.8, and Steffi 4.5. About a third of pre-breeding material was equivalent to cultivar level.

Consumers prefer different levels of mealiness. Nearly 5% of tetraploid blight-resistant clones were slightly mealy; not mealy was absent, and the main part cooked mealy to rather mealy. Standard cultivars were estimated mealier than usually in 2006 due to effect of year and location: Karlena 2.6, Marabel 3.3, Agria 3.2, Jelly 3.2, and Steffi 3.0. About 40% of the earlier tetraploid group and 60% of the later one were only half score more mealy than compared standards. That difference may be compensated by one cross step. Among dihaploid clones only one third cooked mealier than standards.

Medium taste near score 3.0 may be regarded as minimum requirement for table potato on fresh market. Only a third of the earlier group (ese), 8% of the later one and half the dihaploids stayed below this level. Standards were tasted near to it: Karlena 3.4, Marabel 3.2, Agria 3.3, Jelly 3.5, and Steffi 3.0. Improvement of taste is intended in pre-breeding, but appearance, discolouration and disintegration have higher priority. Results of additional tuber traits are continued in table 66.

Beauty of shape of tubers decreases wastage by peeling and entices costumers. Standard cultivars got following results: Karlena 5.8, Marabel 7.8, Agria 7.0, Jelly 8.2, and Steffi 7.3. Nearly three quarter of the earlier (ese) and half the second late group (sla) were scored ≥7 which corresponds with cultivar level. About a third of dihaploids came up to that level (table 66). Examples of a round (fig. 151) and a round-oval pre-breeding clone (fig. 152) are presented. Clone BAZ-GL-01.1396.01 P Sp Ro1 possesses nice oval to long-oval tubers with excellent tuber blight resistance (fig. 153).

Very rough skin characterized long time our most tuber blight-resistant clones. On the contrary, cultivar breeding succeeded to breed varieties with sleek skin. To promote improving of late blight resistance by breeding enterprises sleek skin went an additional breeding goal in our pre-breeding about ten years ago. Clone BAZ-GL-99.8030.05 P (Sp) Ro1 combined very smooth skin with good tuber blight resistance; its table potato quality did not reach the desired level (see fig. 65). Smooth skin, nice round-oval shape, table quality and blight resistance are combined in clone BAZ-GL-99.8084.01 P Sp (St) Ro1 (fig. 154). In 2006 cultivar Karlena got score 5.2, Marabel 7.5, Agria and Jelly 6.3, Steffi 6.7. About 68-89% of pre-breeding material was scored six (rough skin) or better (table 66). The young breeding material shows that this trait can be combined with quantitative tuber blight resistance too; parents for improving by inter-crosses are present.

Discoloration of raw tuber flesh was assessed for nearly 20 years, but with little selection. Score six and better was estimated only on 13-24% of tetraploid and 40% of dihaploid clones. Howev-

er, standard Karlena got 4.1, Marabel 6.7, Agria 4.6, Jelly 4.6, and Steffi 4.7. That level expressed 34 or 46% of tetraploid clones, respectively, and 60% of dihaploids. Pre-breeding goes on to improve this trait. Discolouration of tuber flesh after 24 hours is shown of two clones (fig. 155); BAZ-GL-01.1395.01 P Sp on the left (see pedigrees 9) and BAZ-GL-02.5029.13 P Sp Po Ro1 (see pedigrees 8) on the right side.

Table 66 Part of pre-breeding clones (%) of sub-programme 'blight resistance/table potato' in score-classes of traits important for fresh market in assessment 2006.

Material	Score								
	9	8	7	6	5	4	3	2	1
	Beauty of tuber shape (9 = very beautifully)								
P. i.-resistance, 4x ese	0	26	46	26	2	0	0	0	0
P. i.-resistance, 4x sla	0	8	41	49	2	0	0	0	0
P. i.-resistance, 2x	0	10	28	29	28	5	0	0	0
	Roughness of skin (9 = very smooth)								
P. i.-resistance, 4x ese	0	11	41	37	4	7	0	0	0
P. i.-resistance, 4x sla	0	4	30	34	10	22	0	0	0
P. i.-resistance, 2x	5	14	29	38	0	14	0	0	0
	Discoloration of raw tuber flesh (9 = colour not changed)								
P. i.-resistance, 4x ese	0	7	6	11	22	39	6	9	0
P. i.-resistance, 4x sla	0	0	4	9	21	40	24	2	0
P. i.-resistance, 2x	0	5	10	25	20	25	10	5	0
	Resistance to blue bruise (9 = colour not changed)								
P. i.-resistance, 4x ese	0	4	9	33	33	12	7	2	0
P. i.-resistance, 4x sla	0	0	6	14	44	22	12	2	0
P. i.-resistance, 2x	0	7	29	21	22	14	7	0	0
	Colour of tuber flesh (9 = very deep yellow, 1 = white)								
P. i.-resistance, 4x ese	0	0	4	6	37	35	16	2	0
P. i.-resistance, 4x sla	0	0	0	10	20	37	19	12	2
P. i.-resistance, 2x	0	0	14	10	29	19	23	5	0
	Occurrence of scab (9 = absent)								
P. i.-resistance, 4x ese	72	10	11	7	0	0	0	0	0
P. i.-resistance, 4x sla	60	14	16	10	0	0	0	0	0
P. i.-resistance, 2x	75	15	5	5	0	0	0	0	0
	Occurrence of *Rhizoctonia*-black scurf (9 = absent)								
P. i.-resistance, 4x ese	84	6	2	2	4	2	0	0	0
P. i.-resistance, 4x sla	82	10	2	2	4	0	0	0	0
P. i.-resistance, 2x	75	15	0	10	0	0	0	0	0
	Tuber deformation by *Rhizoctonia solani* (9 = absent)								
P. i.-resistance, 4x ese	86	8	4	2	0	0	0	0	0
P. i.-resistance, 4x sla	92	6	2	0	0	0	0	0	0
P. i.-resistance, 2x	75	10	5	10	0	0	0	0	0

Resistance to blue bruise is assessed for 10 years as an important trait of ware potato quality. An impression of results of assessment after rough peeling represents figure 156. Surprisingly, 46%, 20%, and 47%, respectively, of the three groups of clones obtained score six and better (table 66). Standard variety Karlena got 4.8, Marabel 7.4, Agria 6.2, Jelly 6.2, and Steffi 4.8. This

trait is lesser influenced by environmental conditions than other discolourations and therefore easier to improve. Clone BAZ-GL-00.1186.04 P Sp Kr1 Eca underlines breeding success so far (see fig. 115).

Dominating colour of ware potato tuber flesh in Germany is light yellow to yellow (6) or yellow (7), breeding objective is deep yellow (score 9). Cultivars varied in 2006 from Karlena 5.0 to Marabel and Agria 5.7, Jelly 6.0, Steffi 6.7. However for export and special purposes all colours are usable. Best tetraploid pre-breeding clones were yellow (7) or light yellow to yellow (6), together 10% (table 66). Score five (light yellow) and four (yellowish white to light yellow) dominate among tetraploids. Dihaploids formed more yellow flesh. Sources of late blight resistance and some cultivars used as cross parents with medium late blight resistance expressed white tuber flesh. Backcrosses with cultivars having flesh colour six or seven were highly susceptible to blight and did not result in progeny with sufficient level of blight resistance.

Results of skin colour are not given in detail. About ten years ago grey-brown skin was the rule in our clones with highest level of resistance to *Phytophthora infestans*. Backcross parents were not chosen for shiny skin and according to Kukimura (1972) brown is dominantly over colourless. Progress away from grey brown skin is under way; however, it is too early to decide the combinability of shiny skin with high tuber blight resistance.

Potato crop of 2006 was invaded by scab below normally. Karlena's incidence was scored 7.0, Marabel's 8.5, Agria's 8.0, Jelly's 9.0, and Steffi's 5.2. 60-75% of pre-breeding clones remained free of scab. Higher susceptibility occurred scattered, such clones were eliminated. Similar situation concerned occurrence of black scurf and tuber deformation, caused by *Rhizoctonia solani* (table 66). Deformation was found among dihaploids more often than among tetraploids. Karlena got score seven. Incidence of black scurf differed more, but did not surpass cultivar range: Karlena 6.3, Marabel 5.3, Agria 5.0, Jelly 9.0, and Steffi 9.0.

7.7. Results in combining of resistance to *P. infestans* and *Synchytrium endobioticum*

Wart disease of potato is caused by *Synchytrium endobioticum* (Schilb.) Perc. and is subjected to quarantine legislation. Its spread is not completely prevented by sanitation measures including use of certified seed potatoes and growing of resistant varieties in endangered regions. The soil-borne pathogen is known to develop new pathotypes, which overcome hitherto resistance.

Table 67 Assessment of pre-breeding material with resistance to *P. infestans* of ZL for resistance to potato wart disease.

	Tetraploid clones				Dihaploid clones			
	Wart pathotype 1		Wart pathotype 18		Wart pathotype 1		Wart pathotype 18	
Year	Number assessed	% resistant	Number assessed	% resistant	Number assessed	% resistant	Number assessed	% resistant
1997	43	49	0	-	0	-	0	-
1998	36	83	8	50	6	67	1	100
1999	29	66	16	44	20	40	8	12
2000	38	84	16	19	15	47	8	38
2001	34	82	19	10	13	77	8	12
2002	45	27	11	9	23	52	10	40
2003	104	67	15	27	33	45	1	0
2004	143	76	25	8	16	75	4	50
2005	151	73	43	7	19	13	2	0
2006	146	77	41	15	4	75	2	0

Since 1997 resistance to potato wart has been tested on 10 tubers per pre-breeding clone in BBA at Kleinmachnow or Braunschweig. Simple inheritance of dominant resistance urges to add this trait at the end of the breeding way to only a part of late blight-resistant clones. Table 67 shows that the main part of blight-resistant material is resistant to pathotype 1 of wart and of these about 10% against pathotype 18 too.

We tried to find out where wart resistance in our material originated from. The whole elder material was not tested; therefore present data do not allow sure conclusions concerning utilised wild species. Potato wart disease resistance seems mainly to be originated from crossed cultivars. Beyond that utilised clones of S. bulbocastanum and *S. okadae* possessed resistance to wart pathotype 1 (Darsow 2008).

7.8. Results in combining of resistance to *P. infestans* and potato cyst nematode resistance

Resistance to potato cyst nematodes has high priority in breeding of potato cultivars in opposite to wart resistance. Varieties released in Germany, for instance in 2005, were all resistant to *Globodera rostochiensis* Ro1 und Ro2, 18% to Ro3 or Ro4 or Ro5. Part of pre-breeding material resistant to blight and *G. rostochiensis* improved with increased use of nematode resistant backcross partners because of simple inheritance (table 68). An analysis of available results reveals that resistance to *G. rostochiensis* Ro1, Ro2, Ro3, and Ro5 came in addition from blight-resistant clones of *S. berthaultii*, *S. bulbocastanum* and *S. okadae* (Darsow 2008). In 2006/07 41% of assessed tetraploid clones were combined resistant to late blight and G. *rostochiensis* Ro1. More difficult is it to combine late blight resistance with resistance to *Globodera pallida* pathotype 2 und 3, which is determined by oligogenes. During analysed period the number of tetraploid clones with combined resistance grew continuously (table 68).

Table 68 Number of *P. infestans*-resistant clones, at the same time resistant to *Globodera rostochiensis* Ro1, Ro2, Ro3, Ro5 or *G. pallida* Pa2, Pa3, being tetraploid (4x) or dihaploid (2x). Results of 10 successive years.

Resistance to	Ro 1		Ro2 Ro3		Ro5		Pa2		Pa3	
Ploidy level	4x	2x	4x	2x	4x	2x	4x	2x	4x	2x
1997	5	1	0	0	0	0	0	0	0	0
1998	5	4	0	0	0	0	0	0	0	0
1999	11	2	0	1	0	0	0	1	1	1
2000	5	1	0	1	0	0	2	0	1	0
2001	9	4	0	0	1	0	1	0	1	0
2002	47	9	2	0	2	4	2	2	2	2
2003	79	7	4	0	5	2	4	0	4	1
2004	92	6	10	0	11	1	14	0	14	0
2005	113	4	14	2	15	1	8	0	6	0
2006	139	11	27	1	20	0	20	0	16	0

Resistance to *G. pallida* is mainly intended to combine with late blight resistance for purpose of starch production. However, first clones with combined table potato quality exist as BAZ-GL-01.1555.13P Pa2 Sp Po Kr1 Ro1 Ro2 Ro3 Ro5 (see fig.102).

8. Delivery of BAZ-GL-clones and seeds to cultivar breeding, and production of suitable material for special investigations.

8.1. Pre-breeding for quantitative late blight resistance and cooperation in research

Cooperation in research up to 1991 is mentioned in chapter 6.5.7. In following years expertise of ZL for assessment of late blight resistance on foliage and tubers and suitable material were used in projects with University of Tuebingen (L. Schilde-Rentschler and V. Hemleben, chapter 5.5.). The aim was broadening of genetic basis of resistance in breeding by introduction of genes from new wild species by protoplast fusion. Material developed in it is used nationally and abroad (Schilde-Rentschler et al. 2002, Yermishin et al. 2002).

With CIP, Peru, a project "Improvement of quantitative resistance to late blight of potato for developing countries" was financed by BMZ (German Ministry for Cooperation). This joint project was focussed on application of marker technology for selection of late blight resistance. Our part concerned assessment of blight resistance in long-day conditions, whilst tests in Peru have short-day condition without differentiation of maturity. Additional crossing and application of markers were planned. The project was carried out on PD-population with 246 clones in 1998-2000 with B. Trognitz (Trognitz et al. 2002). In two years average foliage blight resistance of the population of score three was found, and tuber blight scored 3.4 on the 1-9 scale of increasing resistance. This disappointing result was confirmed with progeny of best clones. So it is an example of environmental influence on quantitative resistance and of effect of lateness, which is subtracted in our evaluation.

Transgenic enhancement of often favourable soft rot resistance (*Erwinia carotovora* ssp. *atroseptica*) of late blight-resistant clones (Darsow 1998b, Darsow & Roeber 1998, Wegener 2002) was prepared on four clones. However, the project with C. Wegener, Institute for Resistance Research and Stress Tolerance, IRS Gross Luesewitz, took a rest for political reason.

In „Potato late blight network for Europe", EU-project QLK5-CT-2002-00971, known under EUCABLIGHT mainly experience from application of resistance in breeding could be brought in 2003-2006. The aim of the project was standardization of methods of estimation of host resistance and pathogenicity in Europe (Zimnoch-Guzowska et al. 2005). ZL Gross Luesewitz took part in the field of host resistance. Information and results are available under www.eucablight.org and Colon et al. (2005). Calculation of quantitative foliage blight resistance from primary data was further developed in the project and carried out on latest scientific knowledge in Denmark (Hansen et al. 2006a, b). ZL actively took part in this project (Colon et al. 2004a-d, Zimnoch-Guzowska et al. 2005, Hansen et al. 2006b) and in additions to the database of EUCABLIGHT, which gives more information about R-gene resistance and more reliable information about quantitative resistance to *P. infestans* than other potato databases.

In the complex project "Genetic optimization of the potato by breeding, cell and molecular biology as main donor of starch in the Federal Republic of Germany" the part "Combination of relative late blight resistance to *Phytophthora infestans* of foliage and tubers with increased levels of starch content and not late maturity" was conducted in 2001-2003 at ZL, supported by GFP and FNR. 56 additional cross combinations could be produced and selected in framework of the project. Four inheritors for the desired trait combination were handed over to variety breeders in 2003 (see 6.5.4.3. and 8.3.).

Research in project GABI on late blight resistance of potato in Germany was based on plant material of ZL Gross Luesewitz. InnoNet-project TASK ran since May 2007 to December 2009. ZL took part besides MPIZ Koeln-Vogelsang and breeding enterprises. In sub-project „Resistance to late blight of foliage" was intended to prepare first step of MAS (marker-assisted selection) for quantitative resistance. Four populations with total 854 genotypes were evaluated for foliage and tuber blight resistance (table 69). Breeding stages BC3 (1476) and BC5 (1474, 1475, 1478) were used. Field assessment was carried out 2004-2006 with two replications of three plants each, inoculated with virulence gene combination 1-11 as described under 4.2.3. Collecting of data of disease incidence and of maturity was finished before the beginning of the project.

Table 69 Plant material for research in project InnoNet 5521. Results as three years average.

Population	Ploidy	Parents (1 x 2)	Species included	Maturity 1	Maturity 2	Resistance 1	Resistance 2	Number of clones
1474	2x	BAZ-GL-94.7171.62 x PD163	*phu, dms*	3.1	1.8	7.0	2.8	130
1475	4x	BAZ-GL-94.7082.15 x Delikat	*dms, sto, adg*	5.0	6.3	7.6	2.6	250
1476	4x	GL-Tü-98.02.13 x Leyla	crc	2.9	7.7	8.7	2.5	210
1478	4x	BAZ-GL-93.7015.04 x Delikat	*dms, phu, adg*	5.1	6.3	8.6	2.6	310

Only foliage blight resistance of two populations was considered so far. Highly significant associations of markers were found on chromosome IV and XI with the vertical distance of rAUDPC-values to the regression line with maturity (Truberg et al. 2011). So inheritance of true quantitative foliage blight resistance is confirmed, free of maturity effect. QTL for maturity were found on chromosomes XI and XII.

8.2. Delivery of pre-breeding material for purposes of cultivar breeding

Best pre-breeding clones are offered to breeding enterprises to get new varieties after its use as parental partners with one (for starch) or, more probably, two consecutive cross steps (table potato). Such new varieties with improved quantitative resistance to late blight have to be competitive on the market. Continuously long-term working in both, pre-breeding and cultivar breeding, with good cooperation and adaptation is necessary to succeed in utilization of quantitative late blight resistance. Despite of good pre-breeding, the task of cultivar breeding remains very difficult too.

Delivery of cross parents of ZL-group responsible for pre-breeding material resistant to *P. infestans* is listed in table 70 since 1994. The complex of all assessed traits had to have an acceptable level. Because unsuccessfulness of cultivar breeding endangers existence of private breeding enterprises, and enrichment of negative experience leads to turning away from that type of late blight resistance, only the very best clones at the moment are offered and have a chance of utilization. Not all recipients took over all clones offered, but each offered clone found at least one interested breeder. Each offered clone was described in 44 traits in average of 3-4 years results (mainly score) compared to known standard. Additionally parents and grandparents were recorded. Usually 8-15 tubers were available for each recipient.

Table 70 Delivery of pre-breeding potato clones of ZL (clone names BAZ-GL-….) to German breeding enterprises via GFP.

Year	Number	Ploidy	Traits of special expression, breeding value
1994	4	4x	Resistance to *P. infestans* on foliage and tubers.
1996	3	4x	Resistance to *P. infestans* on foliage and tubers.
	4	4x	Virus resistance, 2 extremely resistant to PVX and PVY.
1997	3	4x	Resistance to *P. infestans* on foliage and tubers.
1999	7	4x	Resistance to *P. infestans* on foliage and tubers.
	3	4x	Virus resistance.
	4	2x	Resistance to PLRV, suitable for table potato and processing.
2001	3	4x	Resistance to *P. infestans* on foliage and tubers, table potato.
	2	4x	Resistance to *P. infestans* on foliage and tubers, suitable for French fries.
	1	4x	Resistance to *P. infestans* on foliage and tubers, starch content.
	2	4x	Table potato.
	2	2x	Processing from cold storage (4°C).
2002	1	4x	Resistance to *P. infestans* on foliage and tubers, table potato.
	4	4x	Resistance to *P. infestans* on foliage and tubers, high starch content.
	2	4x	Starch content and virus resistance.
	3	4x	Processing.
	1	4x	Processing, resistance to *G. pallida*.
	2	4x	Resistance to *P. infestans* on foliage and tubers, table potato.
	4	4x	Resistance to *P. infestans* on foliage and tubers, table potato.
2003	2	4x	Resistance to *P. infestans* on foliage and tubers, processing.
	2	4x	Virus resistance, table potato.
	2	2x	Resistance to *P. infestans* on foliage and tubers, processing.
	2	2x	Processing or table potato.
2004	4	4x	Resistance to *P. infestans* on foliage and tubers, table potato.
	1	4x	Resistance to *P. infestans* on foliage and tubers, processing.
	1	4x	Virus resistance, table potato.
	2	2x	Resistance to *P. infestans* on foliage and tubers, table potato.
	1	2x	Processing, virus resistance.
2005	3	4x	Resistance to *P. infestans* on foliage and tubers, table potato.
	1	4x	Resistance to *P. infestans* on foliage and tubers, processing.
	1	4x	Resistance to *P. infestans* on foliage and tubers, starch content.
	4	4x	Processing.
	3	2x	Resistance to *P. infestans* on foliage and tubers, resistance to viruses and *Erwinia* sp.
	10	2x	Processing.
2006	5	4x	Resistance to *P. infestans* on foliage and tubers, table potato.
	1	4x	Resistance to *P. infestans* on foliage and tubers, starch content.
	4	4x	Resistance to *P. infestans* on foliage and tubers, to *G pallida,* processing, starch content.
	2	4x	Processing.
	1	2x	Processing.
2007	5	4x	Resistance to *P. infestans* on foliage and tubers, table potato.
	2	4x	Resistance to *P. infestans* on foliage and tubers, table potato, processing.
	1	4x	Resistance to *P. infestans* on foliage and tubers, processing.
	5	4x	Resistance to *P. infestans* on foliage and tubers, starch content, processing.
	1	4x	Resistance to *P. infestans* on foliage and tubers, starch content, resistance to *G. pallida*.
	1	4x	Resistance to *P. infestans* on foliage and tubers, table potato, resistance to *G. pallida*.
	1	4x	Resistance to *P. infestans* on foliage and tubers, starch content.

Year	Number	Ploidy	Traits of special expression, breeding value
	3	4x	Virus resistance, table potato, partly suitable for processing.
	3	4x	Starch content, resistance to *G. pallida*.
	2	2x	Resistance to *P. infestans* on foliage and tubers, table potato.
	1	2x	Resistance to *P. infestans* on foliage and tubers, starch content.
	3	2x	Table potato.
	5	2x	Processing.

Among 69 tetraploid BAZ-GL-clones with resistance to *P. infestans* handed over, 27 were more or less suitable to go on to table potato utilization, 17 to processing and 18 to breed new starch varieties. In addition to it, some tetraploid clones were delivered without blight resistance: 13 with high complex virus resistance, 11 for processing, five with table potato quality. Between 16 tetraploid blight-resistant cross parents delivered in 2007, three ripened early, 10 second early, 12 were resistant to *G. rostochiensis* Ro1, two to *Fusarium* sp., three to *Erwinia carotovora*, nine to potato wart pathotype 1, four had improved drought tolerance. For instance in 2003 five late blight resistant tetraploid clones were handed over, from which two were suitable for processing from cold storage at the same time, three were suitable for table purpose, four had good yield and improved resistance to *Erwinia carotovora*, three were resistant to potato wart pathotype 1, two to G. rostochiensis Ro1, two against *Fusarium* caused dry rot.

In 1999-2007 21 dihaploid clones suitable for processing after cold storage (4°C) were handed over to German breeders to contribute to reduction of acryl amide level in future cultivars. This material had another genetic background than most in variety breeding enterprises used chippers related to 'Agria'. Dihaploids with resistance to leafroll virus were asked for and ZL could help from the unusually broad base of pre-breeding in past (table 70). Six of 12 delivered dihaploids resistant to *P. infestans* suited for table purpose, four for processing and one for starch. Three dihaploid clones resistant to late blight on foliage and tubers, to *Erwinia*-soft rot and most viruses were handed over to variety breeders in 2005. Breeding enterprises and Bavarian State Research Center for Agriculture used dihaploids by crossing 2x x 2x or 2x x 4x and by fusion. Mean value of 12 traits allows an impression of delivered material and change of breeding level during about 30 years (table 71).

Table 71 Delivery of ZL clones as inheritors for quantitative resistance to *P. infestans* to German variety breeders. Mean values of 3-4 years assessment in 1-9-scale (9 = desired, very early) or %.

Year	1975-80	81-85	86-90	91-94	96-97	98-2001	02-03	04-05
Number of clones	9	8	15	9	6	17	14	15
Foliage blight resistance in field test	-	-	6.4	6.6	7.3	7.4	7.6	7.4
Foliage blight resistance in leaf test	8.4	8.1	7.5	6.0	7.8	7.4	7.6	7.3
Tuber blight resistance in slice test	7.3	7.1	7.4	6.9	6.5	6.3	6.2	6.1
Tuber blight resistance in test of whole tubers	8.0	7.8	7.9	7.6	7.1	6.8	7.4	7.2
Maturity	2.8	3.0	3.3	3.3	3.8	4.3	4.6	4.7
Yield	4.7	5.0	5.4	6.3	6.4	6.8	6.9	6.6
Juvenile haulm growing	4.2	4.7	5.1	5.8	6.0	6.3	5.8	5.2
Beauty of tuber shape	4.6	4.9	5.5	5.8	6.4	6.6	6.3	6.6
Eye depth	4.3	4.4	4.6	4.8	6.1	6.2	5.9	6.5
Index of table potato quality	3.0	3.5	3.6	4.0	4.6	4.8	5.6	5.2
Starch content (%, bred for starch)	-	-	-	18.9	19.4	20.3	21.9	-
Starch content (%, bred for table potato)	14.9	15.7	16.1	16.4	16.9	16.3	16.0	15.8

For the period shown traits were continuously improved, except tuber blight resistance. That means suitability of pre-breeding material as cross parents increased for the period and probability raised to breed (more) resistant cultivars. Pre-breeding clones delivery to abroad was handled in exchange for material of own interest. From the Netherlands clones with resistance against *G. pallida* were received, from Poland male fertile dihaploids with resistance to *P. infestans* (table 72). However, received clones did only partly correspond to own expectations.

Table 72 Delivery of ZL pre-breeding clones to abroad for breeding purpose.

Number	Traits	Recipient
2	Resistance to *P. infestans*, tetraploid	2000, Cebeco Zaden, 8200AC Lelystad, NL
3	Resistance to *G. pallida,* suitability for processing	2002, VIR St. Petersburg, Russia
2	Resistance to *P. infestans*, pollinators	2003, University Vesprem, Georgikon Agricultural Faculty, Keszthely, Hungaria
2	Resistance to *P. infestans*, dihaploid	2003, IHAR Mlochow Research Center, Poland
1	Dihaploid pollinator	2005, ARC Seibersdorf Research GmbH, A-2444 Seibersdorf, Austria

Tab. 73 Delivery of ZL potato seeds to cultivar breeding enterprises via GFP.

Year	Number of cross combinations	Important traits included
2005	51	Resistance to *P. infestans* and table potato quality.
	14	Resistance to *P. infestans* and high starch content.
	20	Resistance to *G. pallida* and high starch content.
	02	Suitability for processing.
2006	60	Resistance to *P. infestans* and table potato quality.
	12	Resistance to *P. infestans* and high starch content.
	15	Resistance to *P. infestans*, to *G. pallida* and high starch content.
	13	Dihaploids with suitability for processing.
	07	Dihaploids with new sources of resistance to *G. pallida.*
2007	148	Resistance to *P. infestans* and table potato quality.
	43	Resistance to *P. infestans*, suitability for table potato and processing.
	02	Resistance to *P. infestans* and *G. pallida*, table potato quality.
	09	Resistance to *P. infestans* and processing.
	09	Resistance to *P. infestans*, high starch content and processing.
	03	Resistance to *P. infestans* and *G. pallida*, high starch content, processing.
	03	Suitability for processing.
	10	Resistance to *G. pallida* and high starch content.
	28	Resistance to *P. infestans* and high starch content.
	30	Resistance to *P. infestans* and *G. pallida*, high starch content.

Early in 2007 seeds of 10 crosses of wild species x *tbr*, 15 combinations of BC1, 17 of BC2 and 9 of BC3 were delivered to cultivar breeders besides 44 combinations of BC4 and 190 of BC5-6. Immediately before handing-over of responsibility to a successor a part of overhang of seeds and population parts of highly interesting F1 to BC3 were offered. Among these 285 seed families partly additional genes existed for expression of traits of interest: 203 combinations included resistance to *G. rostochiensis*, 111 to *Synchytrium endobioticum* pathotype 1, 27 to *Synchytrium endobioticum* pathotype 18. In 80 seed families increased resistance to *Erwinia sp.* was expected, in 18 families increased resistance to *Fusarium* sp.. Outstanding low susceptibility to damage should be found in 28 combinations. These remarks, parentage of each seed population and the backcross-stage were notified in addition to table 73.

Evaluation report about BAZ-GL-clones delivered to cultivar breeders was given yearly back to ZL. About use of parental clones and outcome of its progeny was informed by H. R. Hofferbert on July 13th 2005 at Gross Luesewitz. Up to 41 000 seedlings descended from BAZ-GL-clones were produced yearly in breeding enterprises in past. Yearly two to 15 clones passed through to C-clones, from which a part was already crossed. In spite of unfavourable inheritance of quantitative late blight resistance most German cultivar breeders are willing to improve blight resistance of new cultivars on that basic. According to cultivar breeders following traits of pre-breeding clones of ZL were emphasized as good expressed: juvenile haulm growing, facility visually to diagnose virus infections, fertility, the level of foliage blight resistance, success of combining foliage blight resistance with second early and early maturity. German breeders were and are highly interested in continuation of potato pre-breeding at ZL Gross Luesewitz.

8.3. Use of pre-breeding potato clones for exhibitions and agronomic practice test

Demonstrations and exhibitions served to announcement of results of applied breeding research in using polygenic resistance type of potato against *Phytophthora infestans* in potato. Since 2003 occasions were used for public announcement as:

1. Growing of resistant ZL-clones in trails to test suitability for ecological farming (several years and several recipients).

2. Show of biological diversity of potato on 'International Horticultural Exhibition Rostock' in 2003, presented at University Kassel, and regional horticultural exhibitions.

3. Exhibition of late blight resistant clones on 'International Green Week' Berlin.

4. Growing show on several regional DLG-field days (fig. 157).

5. Show of current stage in pre-breeding for quantitative late blight resistance on 'European Potato Days', Hameln 2006.

9. Recommendations

9.1. Recommendations to cultivar breeding for using quantitative late blight resistance

Decision to use quantitative late blight resistance in cultivar breeding requires strategic changing for the late-blight part of the breeding programme connected with higher expenditure of work. Seedlings selection is not recommended, but 2-3-years field assessment of foliage blight resistance should comply highest methodical demands and as far as possible should be started with A-clones (in second year of growing in the field) with three plants at minimum. Because of polygenic nature of blight resistance and most other important traits more compromises in selection are necessary at the beginning of each selection cycle and in crosses with low probability to expect cultivar candidates. These compromises relate qualitative and quantitative traits, which are to improve by an additional cross. Qualitative traits as resistance to nematode Ro1 or potato wart disease can easily be introduced by the last cross with another blight and nematode (or potato wart) resistant cross parent.

Because not only backcrossing can be carried out, but at least each second cross step should be an inter-cross of two unrelated, blight resistant cross parents, a (reach) collection of blight resistant clones with nearly cultivar level is to remain for crossing. This precondition decides progress and success of improving of quantitative blight resistance in future cultivars.

Clearly both, the labour-intensive assessment of resistance and the extension of maintaining of cross parents cause higher costs.

9.2. Recommendations to pre-breeding for using quantitative late blight resistance on EU-level and at ZL Gross Luesewitz

Pre-breeding for quantitative late blight resistance of potato in Europe exists a bit on several places in European Union. It is time for ideas on a concept of such pre-breeding responsible for EU. Already the near future will bring more economic pressure to reduce parallel working in different countries. Only the best enforcement enables effective contribution of resistance breeding to protection against late blight in future.

One location of pre-breeding for quantitative late blight resistance should be responsible for EU in a system. Assessment of late blight resistance on seedlings foliage and tubers similarly the practice at Gross Luesewitz is proposed. Later selection stages could be grown and assessed on up to three locations for foliage and tubers blight resistance in parallel. One additional location could produce healthy seed potatoes after the fifth year *in vivo* and *in vitro* (table 74). In the sixth year - the last of assessment of all traits - male and female fertility should be examined and in the following year test crosses should be carried out to estimate the blight inheritance in the eight year.

Table 74 Proposal for selection scheme for resistance to *P. infestans* in pre-breeding in EU.

		Number of plants for					
Year	Clone	propagation	assessment	foliage blight field test	whole tuber test	Tuber slice test	Detached leaflet test
1	Seedling	1	+				
2	Single hill	1-2	+				
3	A-clone	(8-9)	8-9	3			+
4	B-clone	25	15	12, 1 location	6	+	+
5	C-clone	25	15, 3 locationes	12, 3 locationes	6, 3 locationes	+	+
6	D-clone	25	15, 3 locationes	12, 3 locationes	6, 3 locationes	+	+
7	E-clone	25	Crossing and offer of clones for variety breeding				
8	F-clone	15	Progeny test to estimate heritability				

Proposed concentration concerns practical pre-breeding and should be located within a „high grade region", which is officially recognized by EU and a "healthy region" for seed potato production. At the same time pre-breeding has to be located in a region excellently favoured for foliage blight assessment in the field and with tradition in qualified execution. Separation of responsibility for breeding from assessment of resistance has to be avoided. In pre-breeding aspects of plant quarantine and testing for viruses are existentially important. The routine assessment of late blight resistance can include gene bank material and variety candidates too, if highest care is taken to avoid bring in quarantine pathogens. The neighbourhood to a gene bank and research institute is advantageously. Gross Luesewitz and perhaps Ayrshire in Scotland are approved locations of field assessment of foliage blight resistance. Tuber blight resistance should be assessed at the same institutions as foliage blight resistance. Combination with research on the pathogen is partly meaningfully. Global cooperation with research institutes and breeding enterprises should have a more stable and trustworthy partner, if personal and material supply corresponds with the difficult long-term task in sphere of responsibility of EU administration.

In pre-breeding at ZL Gross Luesewitz in JKI is proposed:

1. Instead of tuber slice test from single plants of the first field year the tubers should be used for planting in field assessment on foliage blight resistance (3 plants).
2. ≥60% of the about 300 crosses per year should be intercrosses.
3. In intervals of about 3 years GCA/SCA analysis should be carried out.
4. Marker analysis in potato late blight should be continued at Gross Luesewitz.
5. Breeding on dihaploid level should apply self-compatibility by *Sli*-gene and EBN-mutations (see 6.5.5.).

10. Finally discussion, conclusions and the chances of breeding for quantitative late blight resistance in social context

10.1. Finally discussion

Protection of environment, sustainable agriculture and nutrition of mankind require worldwide much more effective use of genetic resources for durable resistance of potato to *Phytophthora infestans* than hitherto. Durable resistance to late blight of potato is according to present knowledge quantitatively and polygenically. Polygenes for resistance have to be transferred from wild species to cultured potato *S. tuberosum* ssp. *tuberosum*, which is much more difficult than transfer of monogenic dominant genes for hypersensitivity. The genome of wild species contains beside desirable alleles for resistance an excessively large number of undesirable alleles compared with potato cultivars for most of the about 70 traits. Many of these undesirable alleles are inevitable taken over by crossing with a wild donor clone for late blight resistance and have to be replaced through father succession of crosses. That is the very most difficult breeding task, requiring highest level of special experience and pre-breeding in a stable very long-term concept. Where such conditions do not exist, successful utilization of horizontal resistance type can not happen. How do we best evaluate to make sure selecting for best genetic makeup? How do we best breed for durable late blight resistance? Sharing of information is actually more important than sharing germplasm. Therefore this script is offered.

Alternative possibility of plant protection by oomycide application prevented breeding in large parts of Europe and whole North America from consequent use of quantitative resistance since in the 1970ies the use of qualitative late blight resistance was abandoned. The present knowledge of polygenes is in its infancy, so a method of cut out these genes and their clean transfer into potato cultivars might be available for breeding perhaps in far future. Nevertheless, conventional breeding is able to replace undesirable alleles by systematic breeding in a series of crosses. How that can be managed is here described for long-day conditions. The results in ZL Gross Luesewitz are much better than expected, but are not generally known, because German breeders like to use the advantage imperceptible; institutions and breeders abroad probably distrust our results, which might undermine their reputation. Additionally our results reverse main arguments for application of gene technique research for late blight resistance. Our expectation to replace a third of current fungicide demand by improved level of quantitative late blight resistance, provokes great antagonists. On the other hand, organic potato production required several decades to understand that such pre-breeding as at ZL Gross Luesewitz is essentially for their continuation. In the Netherlands organic potato breeding is tried with farm-breeders in cooperation with Agrico (Lammerts van Bueren et al. 2008).

Internationally unusual success of our pre-breeding for quantitative late blight resistance was enabled by a complex of conditions and decisions. Research of the Institute for Potato Research Gross Luesewitz was consequently focussed on reliable protection against loss by foliage and tuber blight in agricultural practice. Practical success had priority over publication. Quantitative resistance was selected as basis of breeding in 1964 after development of suitable methods for large scale selection. Additional methods have been adapted and priority of blight resistance in selection system was realized. Separation from cultivar breeding, but good cooperation with cultivar breeders, helped to consider all important traits from the beginning and pay attention on different traits to the right time depending from its inheritance. Responsibility of one person for both, the pathological and breeding part of the work was usefully because of complete integration of aspects of pathology and breeding. Separation of maturity effect on disease incidence followed from internal analyses and was applied since about 30 years in pre-breeding (Darsow 1989b). Resistance calculated with the empirical method correlated with

that calculated by regression to maturity r = 0.9 (Darsow & Strahwald, not published). Because last method separates maturity effect completely, our breeding progress is understandable. Each breeding for quantitative late blight resistance for long-day has to run aground without this methodical separation as it did in several countries. None biometric method of calculation without this central intention can help any step forward and therefore the patience with this difficult type of resistance is partly lost.

Strong selection of resistance donors in our pre-breeding included several years' evaluation and application of highest of all available virulence gene combinations of inoculum used. In contrary to our strategy, short selection and quick crossing is commonly with the same effect as building on sand. Genes of diverse resistance sources have to be transferred at the same time to get a genetic broad basis of pre-breeding material. The sources should be searched first line in accessions from regions with highest native selection pressure for late blight resistance according to Budin (2002). Since quantitative resistant variety-near clones have low percentage of progeny with good level of combined foliage and tuber blight resistance, diverse populations with at least 600 seeds each are necessary, i.e. pre-breeding for quantitative resistance has only a chance on large scale, which is not realized anywhere today. This enables to combine different genetic backgrounds through crosses resistant x resistant, using additive and specific combining ability and avoiding dropping under a critical resistance level before improving of other traits succeeded. Such crosses might be BC2 x BC4, BC3 x BC4, BC3 x BC5 or similarly to improve traits in pre-breeding stock without loss of late blight resistance. Progress in improving table potato quality of blight resistant clones with sleek skin requires large-scale inter-crossing, which is not possible for a small research group. However, new possibilities exist for breeding progress on diploid level by exploiting the *Sli*-gene (Lindhout et al. 2011) and Mexican sources (Yermishin et al. 2002, 2011). Continuously new sources of resistance are exploited at ZL in small extent and added to the present material to counteract adaptation of the pathogen population in the far future by using additional "new" (desired different) polygenes for resistance.

Best pre-breeding clones are offered to breeding enterprises to get after its use as parental partners with one (for starch) or two consecutive cross steps (table potato) new varieties, competitively on the market with improved quantitative resistance to late blight. Continuously long-term working in both, pre-breeding and cultivar breeding, with good cooperation and adaptation is necessary to succeed in utilization of quantitative late blight resistance. Despite of good pre-breeding, the task of cultivar breeding remains difficult. Results of ZL show that quantitative late blight resistance can be combined in principle with all other traits of interest by conventional breeding. However, successful use of quantitative late blight resistance in variety breeding requires more than considering two additional traits (foliage blight and tuber blight resistance). It requires changing of trait priorities and of selection procedure in a part of the breeding programmes and causes quantitatively reduced chances to find a new variety. With that, a difficult and more costly but practicable way exists alternatively to gene technique to reduce oomycide application to about two third in interest of environmental and consumer protection.

Because of necessity for identification of races of *P. infestans* and for identification of R-genes in future too it is necessary to continue this part of routine with required attention and means. In most countries these tasks can only partly be exercised due to saved expense.

Recently governmental financing and continuation of potato pre-breeding at Gross Luesewitz was decided to continue in affiliation to the German Federal Ministry of Food, Agriculture and Consumer Protection. A location as Gross Luesewitz really only enabled efficient working with wild potatoes in breeding, because it is located in the "healthy region for seed potato production in M-WP" and at the same time within the „high grade region", which is officially recognized by EU and protects additional against introduction of harmful organisms. Several years' growing of segregating populations or wild cross parents was possible only here without seed

production from *in vitro* culture. For field assessment of foliage blight resistance special microclimatic favourableness in this place is also obviously.

Whilst CIP is successfully in late blight resistance breeding for short day conditions, existing demand for long-day conditions can internationally not be met. It concerns the main part of world potato production: Europe, North America, Argentina, Chile, South and North Africa, Turkey, Iran, Iraq, Afghanistan, Pakistan, China, Russia and other. Correspondingly high interest exists in material and concept of ZL, which should be used for cooperation. Possible contribution to nourishing of future world population and to conservation of environment highly motivates continuation of the pre-breeding at Gross Luesewitz.

Here given results will affect international basic research for quantitative foliage blight resistance too. Genetic interpretations of relation between foliage blight resistance and maturity are based mainly upon disease incidence data, which express a mix of maturity effect and real resistance. Hence it follows that the term resistance is mainly in incorrect usage. Application of suitable, here proposed method should finish that insufficiency.

10.2. Conclusions for utilization of quantitative late blight resistance

Following conclusions are drawn:

- Process of identifying of wild donors of quantitative resistance, its introduction into and stable establishing in genome of cultural potato by combining with quality, yield, early maturity and a lot of other traits is a very difficult long-term task. It requires very complex pre-breeding, enables progress only in little steps, and presupposes very long-term planning and financing.

- In opposite to common opinion combining of quantitative resistance of foliage and tubers to *P. infestans* with all other traits succeeded in pre-breeding on tetraploid level at ZL Gross Luesewitz. With that a difficult but practicable way exists. The new possibility in overcoming self-incompatibility should open additionally effective contribution from pre-breeding on diploid level.

- It is expected to reduce oomycide application in interest of environment and consumer protection to about two third by new cultivars bred with parental clones of ZL.

- Priority of late blight resistance in selection system has to be realized. Influence of environment, plant age and tissue-specific expression are to consider. Decision about elimination of clones has to be done for quantitative traits mainly on several years' average.

- Compatibility of inoculum to the test material is to assure as basic requirement in assessment of quantitative late blight resistance by inoculation.

- Foliage blight resistance has so to be calculated that it is not correlated with maturity.

- In variety breeding utilization of quantitative late blight resistance is connected with some changing. Priority of crossing resistant x resistant requires a collection of blight-resistant genetic diverse parental clones and changed selection scheme. Reduced probability of progeny with cultivar level requires enlarged seedlings populations and maintaining of a collection of inheritors for late blight resistance.

- On EU-level one location of pre-breeding for quantitative late blight resistance is proposed to be responsible in a system with two to three locations for assessment of foliage and tuber blight resistance. One additional location should produce healthy seed potatoes *in vivo* and *in vitro*. The pre-breeding has to be located in a region excellently favoured for foliage blight assessment in the field, in a region with lowest risk to be affected with potato diseases, and with tradition in qualified execution. National responsibility has to change in sphere of responsibility of EU administration.

- Worldwide high demand for durable resistance to *Phytophthora infestans* and the possible contribution to nourishing of future world population and to conservation of environment make pre-breeding for quantitative late blight resistance a permanent task with high social priority.

- The main part of known statements about relation of QTL for late blight resistance of potato foliage and maturity is to scrutinize because the methods used were mainly unsuitable for that purpose.
- Possibilities for assessment of qualitative pathogenicity (avr-genes) and quantitative pathogenicity (aggressiveness) of isolates, its maintenance and making identified pathotypes available for breeding purposes is a permanent task.
- The available set of differentials should be further developed to a better comparable level concerning its maturity, growing habit, the quantitative late blight resistance level and the facility visually to diagnose virus infections. Inclusion of new R-genes is necessary.

10.3. Social trends and the use of late blight resistance types

Potato could more contribute to nourishing of mankind today and in future, but only with increased durable resistance to late blight (Niederhauser 1999). Quantitative resistance of potato against *P. infestans* would more than in past help to conserve environment, sustainable to grow potatoes and to preserve human health. For this type of resistance the demand is globally very highly, but several powerful interests on the market are striving successfully against it and several circumstances conflict with it.

A strong reduction in public paid crop-oriented research is obtained in agricultural science and additionally in orientation to solve practical problems in the public and global interest (Struik 2006). Successful using of fungicides gave reasons for not enough research on this difficult type of resistance and its application in breeding. The methods of assessment were not appropriate enough and the breeding system was not conductive to get new varieties more resistant. More negative experience was accumulated than success with the time-consuming, labour-intensive and difficult to handle quantitative resistance at the beginning. Saving of labour costs is a current trend. Quantitative resistance based on polygenes from wild potato species and its use requires conditions quite different from the modern trend in science, business and politics: long-term planning (several decades), high education in breeding, pathology and physiology, long-term experience, high personal engagement to the long-term aim, perseverance, reliable long-term financing. The stable good breeding progress in pre-breeding for combining high quantitative late blight resistance with quality traits at ZL Gross Luesewitz is very rarely quoted in literature (Monti & Struik 1999, Swiezynski & Zimnoch-Guzowska 2001), probably because of the contrast to the common expectation, and moreover, because of disturbing arguments in support of resistance breeding with GMO's as well as because of interfering with intensive application of oomycides.

Breeding for late blight resistance since a few years is about to go away from quantitative resistance and turn again to plant protection industry-supported application of the hypersensitivity. The same step was taken about 100 years ago with disappointing results; however, now gene technique is expected to enable quicker and more flexible reaction in race against the pathogens adaptability in opposite to only conventional breeding in past. Umaerus and Umaerus (1994) wrote: „The hope now is that information on resistance mechanisms may give rise to more accurate predictions which allow the choice of the best type(s) of resistance as well as the most efficient breeding method." Is genetic engineering in breeding the better method? From which point of view this is decided? Who takes responsibility for the decision? Answers are not given by independent science but from the winners on the market.

Why do we have such situation? There was not enough public interest or power to replace oomiciyde application earlier. Today the big players of chemical plant-protection industry are the big players of gene technique. The reality has its own way influenced from market regulation and most profitable solutions. In the genomics era the hopeful principle of quantitative resistance has globally quite insufficiently scientific and public reputation and support. There is too less reliable information.

Following social trends influence the chances of using quantitative late blight resistance: General public has mainly lost contact with and understanding for food production and agricultural science (Struik 2006). Scientists are increasingly dependent on lender of money, which is allocated at short notice for short duration. Politicians as scientists apply short-term strategies. How is responsibility taken for best long-term solutions for people or environment? In breeding research present-days specialists partly feel conventional breeding as numbers game (Innes 1995). Understanding between cultivar breeders and researchers seems more and more difficult. Genotypic selection often is expected in breeding based on only preliminary knowledge, acting in only restricted part of the material and only possible for one or few traits. The main argument for application is saving of time, but that is not compatible to selection in all, which has to consider many traits at the same time. Nevertheless, scientific progress strengthens the future basis of breeding, but only with balanced steering. Who does it? The majority of resistant varieties have been developed without clear understanding of the genetics or mechanism of resistance involved (Russel 1978).

Molecular-genetic methods are more suitable to application on simple qualitative resistance type; interpretations of the complex and variable phenomenon of quantitative resistance are predominantly not possible at the moment. On the contrary, results with hypersensitivity type of resistance (R-genes) are possible from short projects. Breeding progress is much quicker using this race-specific type of resistance. However, there is reasonable doubt, that durable protection can really be managed on this basis. In producing the GMO-clones in the Netherlands DuRPh project about 49% were stated to deviate from the type of the cultivar used, but not all traits were compared (Hutten et al. 2010). Heeres et al. (2002) required 1,000-5,000 explants to be set up in order to obtain 10 plants with expected target trait expression and true to type phenotype. Only five from 500 rooted GMO-shouts showed expected active reaction of three transferred R-genes combined (Zhu et al. 2010). The molecular genetic handling is not as predictable as it is described usually (Zhong 2001). It is very disquieting, how the new concept using R-genes for late blight resistance is substantiated (Muskens & Allefs 2002, Allefs et al. 2005, Haverkort et al. 2008). Terms as "broad-spectrum resistance" (van der Vossen et al. 2005) or expected "durable resistance" or "durable resistance strategy" (Haverkort et al. 2008) are now used for new detected R-genes or the intended system of its using to give the impression of a quite new quality of resistance due to scientific progress, but the broad effect is no more than a hope, a picture at the beginning of the host-pathogen relation prior the possibility of pathogens adaptation in potato growing. In principle, research connected with GMO's is much lesser public than usually and accompanied with protection of knowledge as instrument in the competition for market share. The intended diversification of GMO-cultivars in time and locally suggests that the initial expectation of durability of GMO-constructs is partly lost (Kessel et al. 2010). The permanent production and systematic diversification of GMO's is very expensive, highly susceptible to trouble and will lead to only few grown varieties on a very high part of potato acreage, which will include an additional risk for becoming ineffective by adaptation of other pathogen populations and pests besides of *P. infestans*.

Private patentees push this development, which has the potential to guarantee monopoly of seed potato production world wide. Only an initial success is necessary to establish this breeding technology with tremendous social side effects, because potato is basic food produced partly by traditional small holders in large parts of the world (Coffey 1991, Ezekiel & Shekawat 1999, Forbes 1999, Govinden 1999, Jansky et al. 2009a, Johl & Dahiya 1999, Singh 1999b, Rogozina et al. 2001, Simakov & Anissimov 2006, Wagoire 2011). Coexistence with conventional growing or ecological farming seems imaginable only in separated different regions. About the quite new situation for farmers has not been spoken resulting from patents on the gene-engineered modifications of known cultivars. Radical consequences for present breeding enterprises are expected.

Are there gone steps to generally gene engineering-based breeding without social consensus? The far-reaching and high-risky decision for potato late blight resistance breeding with R-genes by MGO's is hardly to turn back. One risk is linked with acceptance by consumers, which will globally be decreased by the initial prize. Easier acceptance to the public is assumed because of applying potato genes (cis-genes) without additional markers. Struik & Wiersema (1999) wrote: "The introduction of genes through genetic engeneering is not completely without risk and may affect nutritional and other properties affecting human health". Are really all unintentional and unforeseen effects tested and excluded? Who tested how and how long which effects? The application of transgenic cultivars with qualitative late blight resistance is intended first of all outside of Europe (see Zhu et al. 2010).

11. Summary

This script informs about importance of late blight in potato, explains both types of resistance, and discusses factors influencing resistance expression. The state of research on pathogenicity of *P. infestans* as well as on resistance on foliage and tubers is reviewed. Epidemiological aspects in assessment of late blight resistance, its stability and the strategy of its use are comprehensively considered. Breeding for late blight resistance in past and present is analysed and reasons for mainly globally insufficient results are given on the background of about 45 years successful pre-breeding under long-day conditions at JKI Gross Luesewitz. Social aggravations for using polygenic resistance are mentioned.

The known methods of assessment of foliage and tuber blight resistance are rewieved and partly annotated. Higher demands are necessary in methods of assessment, which are mainly internationally insufficiently fulfilled. Evaluation of genetic resources of tuber-bearing potato collections is critically estimated; international use of potential donors of resistance is listed for some countries. More effective search of sources of resistance is recommended.

The own strategy in assessment of resistance and breeding and own results in pre-breeding up to retirement of the author are presented on about a third of the pages. 33 pedigrees illustrate the breeding successions. 74 tables present results; 157 figures illustrate methodical details, show results or pre-breeding clones. The given results prove that quantitative blight resistance on foliage and tubers can be combined with all desired traits of potato including earliness and quality. This is just the opposite of the teaching of science and experience of majority of variety breeders. It is the intention of this script to change that by sharing information and communicate the know-how. The very extensive number of about 1400 references facilitates information in elder or ignored literature and may reduce repeated research.

Pre-breeding for quantitative blight resistance caused by minor genes requires another assessment practice of resistance and breeding strategy than for use of dominant major genes. Reasonable methods of large-scale screening of resistance were developed and suitable breeding conception was applied systematically at ZL Gross Luesewitz. The main problems of this pre-breeding and their solutions are discussed. 197 accessions of 42 *Solanum* species were used by producing of seeds and starting selection of next parental generation over the years. Usually several genotypes of an accession were used as cross parents. As much as possible traits were tested several years besides blight resistance of foliage and tubers in wild potato clones too. The whole of the expression of all the traits decides to reject or to use a potential source of resistance or clones of its progeny as cross parent. Sources of resistance were exploited by crossing or by protoplast fusion. High susceptibility to virus diseases (PVY mainly, PLRV) frequently caused premature loss of wild clones or its progeny. Cross parents with very high resistance to viruses were used therefore at the beginning. Other undesirable negative 'wild' effects were reduced by following backcrossing and inter-crossing (resistant x resistant).

68 traits were considered in pre-breeding for quantitative late blight resistance; the methods of assessment of these traits and the scheme of selection are described. An important role played inter-crosses preferred of not related clones to resist loss of genes for blight resistance in meiosis. It is essentially to improve other traits by inter-crossing at the same time. Given results show that in our genetic broad based blight-resistant material enough variance for most traits was produced by suitable cross planning. Progress in polygenic or oligogenic traits occurred in little steps and requires planning of crosses beginning with wild species and beyond several generations. A series of at minimum eight cross steps will be necessary from the wild species to a new variety. It is necessary to decide the utilization of a blight resistant clone for processing, table potato or starch as early as possible.

The data of expression of 64 traits of 248 tetraploid and 61 dihaploid clones, grown in 2006, demonstrates the state of the progressed part of pre-breeding for late blight resistance at the ZL Gross Luesewitz. Slow, constant progress is shown in the most difficult part too, the combining with table potato quality. Some clones reached the level of good cultivars and give better preconditions to go on than in past. Above all, discolouration after cooking and uniformity of tuber size are to improve. Additionally a sub-programme is running to combine high starch content with blight resistance, earliness, resistance to *Globodera pallida* Pa2 and Pa3, *G. rostochiensis* Ro1 and *Synchytrium endobioticum*. Combining of suitability for processing and blight resistance has better results concerning French fries than crisps.

Three methodical variants to assess maturity were conducted in parallel, results are offered. About 6% of the late blight resistant pre-breeding clones grown in 2006 were very early, 14% were early, 20% between early and second early, 31% second early, 19% second early to second late and 10% second late. The mathematical separation of the part of true late blight resistance of foliage from the effect of maturity (lateness) on disease progress is a primary condition of appropriate selection for foliage blight resistance. Sufficient genetic variance of resistance was ascertained in the pre-breeding material of ZL in JKI at Gross Luesewitz, even, if it was calculated as vertical distance of rAUDPC to the regression line with maturity ($h^2 = 0.768$).

Pre-breeding for blight resistance was conducted mainly on tetraploid level. Absence of male fertility in blight resistant dihaploids allowed only crosses resistant x susceptible up till now. So advantage of breeding on diploid level could not be exploited. Some clones were used by fusion on tetraploid level. Newest possibilities to introduce self-compatibility should be used.

69 tetraploid blight-resistant cross parents were handed over to cultivar-breeders since 1994, among them 27 usable for table purpose, 17 for processing and 18 clones for starch production. Six of 12 blight-resistant dihaploids were suitable for table potatoes, four for processing, and one for starch. Beyond that, seeds of 477 cross combinations with 100-900 seeds each were offered in 2005-2007. These parental clones are expected to become parents or grandparents of new varieties, which are expected to save 33% of current oomicide use in growing. The internationally leading state of ZL Gross Luesewitz in pre-breeding for quantitative blight resistance for temperate climate and long-day conditions should be maintained and used for cooperation with countries as China, South Africa, Australia, Argentina, Chile, Canada, Russia, and other.

Cooperation in research concerned broadening of basis of used sources of resistance and application of new methods (University Tuebingen) or introgression of marker-assisted selection for late blight resistance (CIP Lima). Acceleration of combining starch content with resistance of foliage and tubers and not late maturity was realized in a national project. Harmonizing of methods of late blight resistance assessment in Europe could be advanced in project EUCABLIGHT. Since decade's foliage and tuber blight resistance of gene bank GLKS of IPK Gatersleben was tested by the same group of ZL at Gross Luesewitz.

Continuation of pre-breeding for quantitative late blight resistance of potato in departmental research of Federal Ministry of Food, Agriculture and Consumer Protection is legitimated by its potential contribution to environmental and consumer protection, by the breeding results

up till now, by world-wide shortage of blight resistant pre-breeding material and cultivars, by necessity to counteract the loss of genes in potato breeding and by the demand on suitable potato material for basic and applied research. Conclusions for utilization of quantitative late blight resistance in future and recommendations are given for concentrated organization of pre-breeding for late blight resistance on potato in EU.

Acknowledgements

Pre-breeding for quantitative resistance of potato to *Phytophthora infestans* (Mont.) de Bary at Gross Luesewitz was started under direction of Prof. Dr. Rudolf Schick in 1964 by Dr. S. Jeschke and continued by Dr. H. Oertel; in 1972 the author became responsible. Interruptions by later directors could be prevented. Present keeping on of pre-breeding with potato at Gross Luesewitz is to owe to Prof. Dr. P. Wehling and Prof. Dr. G. Backhaus. Technical assistant Mrs. K. Boehm und skilled worker Mrs. U. Dominik have contributed to successful outcome by diligent and circumspect employment of their reach practical knowledge. I thank Mrs. Dr. K. Sonntag and Dr. R. Thieme for taking up of clones in vitro culture, protoplast fusions, and assessment of ploidy level. The group of workers in field trails and its leader extensively supported the pre-breeding. Good co-operation occurred with Dr. H. U. Juergens in a project to acryl amide; friendly help of many colleagues is remembered.

The author want to express his gratitude for co-operation to E. Hinze, Dr. K. Schueler, Dr. K. Dehmer and its colleagues from gene bank, to Mrs. Dr. L. Schilde-Rentschler, University Tuebingen, concerning fusions, to Mrs. Dr. I. Wulfert, Dr. J. Kruse, Mrs. Dr. Walter from Department Plant Protection of Office for Agriculture, Food and Fishery Mecklenburg-West Pommerania at Rostock, concerning assessment of nematode resistance and tests for quarantine organisms. Mrs. Dr. B. Schoeber-Butin, Mrs. Dr. Plath, Dr. F. Niepold, Dr. H. Stachewicz, and Dr. Langerfeld from the former BBA Braunschweig kindly provided with suitable isolates of *P. infestans* and/or assessed resistance to *P. infestans* (additional tests some years), to *Synchytrium endobioticum*, to *Erwinia carotovora* or to *Fusarium coeruleum* on tubers.

I thank breeders and managing directors of breeding enterprises for co-operative and critical company in breeding aspects, the colleagues of GFP for co-operation in projects and meetings. The pre-breeding was continuously financed by the German Federal Ministry of Food, Agriculture and Consumer Protection.

Mrs. Dr. I. Wulfert kindly supported the script by valuable comments after critical reading.

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13. Abbreviations used

ABPT	cross succession ([([*acl* x *blb*] doubled by colchicine) x *phu*] x *tbr*)
ABPTT	cross succession [([([*acl* x *blb*] doubled by colchicine) x *phu*] x *tbr*) x *tbr*]
acl	*Solanum acaule*
adg	*Solanum tuberosum* ssp. *andigena*
AIR	**a**pparent **i**nfection **r**ate, slope of the disease progress curve
AUDPC	**a**rea **u**nder the **d**isease **p**rogress **c**urve
AULEC	**a**rea **u**nder the **l**esion **e**xpansion **c**urve
blb	*Solanum bulbocastanum*
B	$B=r^2$, certainty of explanation of one trait from variance of another
BAZ	Federal Centre for Breeding Research on Cultivated Plants, renamed to Julius Kuehn-Institute Quedlinburg in 2008
BAZ-GL-	Clones handed over to cultivar breeders or other institutions are named that way up to 2007.
BAZ-GL-Tueb-	Clones from protoplast fusion of a wild species with *tbr*-clones produced at University Tuebingen, tested, selected and used at ZL Gross Luesewitz
BC1… BC4	first … fourth backcross of interspecific cross to *S. tuberosum* ssp. *tuberosum*, explained in table 35
BFR	index of tuber blight resistance of assessment of whole tubers freshly harvested
BGRC	Dutch-German Gene Bank
chc	*Solanum chacoense*
cmm	*Solanum commersonii*
crc	*Solanum circaeifolium*
cv., cvs.	cultivar, cultivars
diha	dihaploid
dms	*Solanum demissum*
DPC	**d**isease **p**rogress **c**urve
ea	**e**arly **m**aturing
EAPR	**E**uropean **A**ssociation for **P**otato **R**esearch
Eca	resistant on tubers to soft rot caused by ***E****rwinia* ***c****arotovora* ssp. ***a****troseptica*
ELISA	**e**nzyme-**l**inked **i**mmuno**s**orbent **a**ssay, a method to detect viruses
ese	maturity from very **e**arly to middle of **s**econd **e**arly
F1	progeny of interspecific cross
FNR	Coordinating Institution for Growing Raw Materials (Fachagentur fuer Nachwachsende Rohstoffe) at Guestrow, Germany
GABI	German plant genome initiative
GFP	Society fuer Plant Breeding, Gesellschaft für Pflanzenzuechtung e.V. at Bonn
GISH	**g**enomic ***in s****itu* **h**ybridisation
GL	**G**ross **L**uesewitz near Rostock, location of potato research and breeding as IPZ, IK, ILK, ZL, respectively, belonging to BAZ since 1992 and JKI since 2008. Abbreviation in designation of breeding clones since 1949.
GL-I-	designation of breeding clones from station Gross Luesewitz, synonymous Lü.
GL-II-	designation of breeding clones from station Lindenhof, synonymous Li.
GL-III-	designation of breeding clones from station Karow, synonymous Ka.
GL-VI-	designation of breeding clones from department Pre-breeding
GLKS	Potato gene bank of IPZ, later IK Gross Luesewitz up to 1991, of IPK Gatersleben at Gross Luesewitz since 1992

GMO	**g**enetically **m**odified **o**rganism
GT	**g**eneration **t**ime
hjt	*Solanum hjertingii*
IE	**i**nfection **e**fficiency
ILK	Institute of Agricultural Crops Gross Luesewitz, renamed to Institute of Breeding Research on Agricultural Crops, ZL in 2008
IPK	Institute of Plant Genetics and Crop Plant Research Gatersleben
IT	**i**ncubation **t**ime
JKI	**J**ulius **K**uehn-**I**nstitute, Federal Research Centre for Cultivated Plants, Quedlinburg
Kr1	resistant to potato canker (*Synchytrium endobioticum*), pathotype 1
Kr18	resistant to potato canker (*Synchytrium endobioticum*), pathotype 18
la	**la**te maturing
LGR	**l**esion **g**rowth **r**ate
LSD	**l**east **s**ignificant **d**ifference
mag	*Solanum maglia*
MAS	**m**arker-**a**ssisted **s**election
MPI-	**M**ax **P**lanck-**I**nstitute
M-WP	**M**ecklenburg-**W**estern **P**ommerania, country of Germany
phu	*Solanum phureja*
oka	*Solanum okadae*
opl	*Solanum oplocense*
Pa2, Pa3	resistant to White cyst nematode *Globodera pallida* pathotype 2, pathotype 3
Pe	clone particularly low susceptible to damage (injury) of potato tubers
P. i.-resistance, 4x ese	clones resistant to *Phytophthora infestans*, tetraploid, **e**arly to **s**econd **e**arly maturing
plt	*Solanum polytrichon*
Po	suitability for production of French fries
PPO	**p**oly**p**henol **o**xidase
pta	*Solanum papita*
PT	**p**enetration **t**ime or inoculation period
QTL	**q**uantitative **t**rait **l**ocus
r	correlation coefficient
rAUDPC	**r**elative **a**rea **u**nder the **d**isease **p**rogress **c**urve
R-gene	gene for monogenic dominant race-specific resistance (qualitative resistance)
RH	**r**elative **h**umidity
Ro1	resistant to golden cyst nematode *Globodera rostochiensis* pathotype 1
Ro2 … Ro5	resistant to golden cyst nematode *Globodera rostochiensis* pathotype 2 …5
S.	*Solanum*
SC	**s**porulation **c**apacity
SCRI	**S**cottish **C**rop **R**esearch **I**nstitute Dundee
se	**s**econd **e**arly maturing
se-sl	**s**econd **e**arly-**s**econd **l**ate maturing
sl	**s**econd **l**ate maturing
sla	maturity group including second part of **s**econd early to very **la**te
SP	suitability as table potato
(SP)	limited suitable as table potato

spg	*Solanum speggazinii*
St	high starch content
sto	*Solanum stoloniferum*
tbr	*Solanum tuberosum* ssp. *tuberosum*
Tt	drought tolerant
UGPase	**U**-**G**lucose **p**yrophosphoryl**ase**
Vac Inuv	**V**acuolar **ac**id **inv**ertase
ve-ea	**v**ery **e**arly-**ea**rly maturing
ver	*Solanum verrucosum*
vrn	*Solanum vernei*
ZL	Institute of Breeding Research on Agricultural Crops Gross Luesewitz - formerly Institute of Agricultural Crops Gross Luesewitz (ILK) - formerly Institute for Potato Research Gross Luesewitz (IK) - formerly Institute of Plant Breeding (IPZ)

14. Terms explained

accession	sample of tubers or berries of a (potato) plant collected on its native habitat;
accumulating breeding	bring together of genes for a trait from both parents; repeated intercrossing;
A-clone	breeding material in its second year on the field, its third year after sowing;
aggressiveness	quantitative pathogenicity, determined in comparison to other isolates;
AIR	**a**pparent **i**nfection **r**ate = slope of the disease progress curve;
backcross	explained in table 35;
BAZ-GL-01.1446.02 P se	designation or name of pre-breeding potato clones of JKI from Gross Luesewitz up to 2007. Year of sowing was 20**01**; it follows the number of the cross family **1446**, from which here clone **02** was kept. The clone number following **P** stands for late blight resistance on foliage and tubers, **se** means second early. Such additions give short information on the value of a clone and are recorded under **Abbreviations used**.
B-clone	breeding material in its third year on the field, its fourth year after sowing; each following letter means one year elder;
cis-genes	gene complexes transferred by gene technique from other potato species into a cultivar or plant belonging to *Solanum*;
combination breeding	bring together of genes for different traits by different parents;
compatible host-pathogen relation	in this interaction no R-gene protects the host, disease can follow;
conventional breeding	producing new gene combinations by crossing, protoplast fusion or inducing mutations followed by selection of new cross parents or a new variety out of the progeny;
differentials	group of potato clones, each with another known R-gene or R-gene combination used to determine the virulence genes of *P. infestans* isolates by assessing
double pollination	pollination with a helper pollen and additional the intended pollen, which alone is not successfully;
embryo rescue	dissection of few days old embryo and its cultivation *in vitro* to escape abortion;
field resistance	this term does not include guarantee for or knowledge of the acting type of resistance;
gene bank	public institution for cultivation, propagation, evaluation and long-term storage of samples of plants;
hypersensitivity	a principle of resistance based on quickly locally becoming necrotic of infected cells which includes dying of the pathogen;
inter-cross	crossing of two parents which both contribute to the target trait, for instance late blight resistant x late blight resistant;
in vitro	cultivated on artificial medium;
in vivo	normal growing;
Irish famine	great period of hunger caused by late blight of potato 1845-1848;
molecular map	arrangement of localised genes in defined parts of the chromosomes;
mutation breeding	inducing of mutations and selection of cross parents from it
NB-LRR-genes	class of genes encoding **n**ucleotide **b**inding and **l**eucine **r**ich **r**epeats domains;
oomycides	"fungicides" effective against oomycetes, which are not fungi;

pedigree	genealogical tree of a clone. Details are explained in chapter 5.4.;
polygenic determined	many genes take part in expression of the trait;
pre-breeding	breeding to produce cross parents adapted for use in cultivar breeding. About 45% of alleles in F1 of interspecific cross have to be replaced by pre-breeding in a long series of crosses in case a wild specie is exploited as source for improving a trait. About 3-4 % have to be replaced there after
predisposition	exogenic and/or ontogenic modification of the genetically determined resistance behaviour;
protoplast fusion	plant cells without its wall are unified by means of electric impulse; intended is combining of two cells of different clones (species);
race of *P. infestans*	characterisation of qualitative pathogenicity by its virulence;
saturation crosses	for target trait 'resistance' crossing of ((resistant x resistant) x resistant), repeated inter-cross;
somaclonal variation	variation of clones which are descended from identical somatic tissue, caused by *in vitro* conditions;
transgressive segregants	single clones of the progeny which exceed the best parent;
trisomic nucleus	nucleus (of *P. infestans*) with additional chromosome(s);
virulence	qualitative pathogenicity, determined by means of differentials;

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16. Figures

Fig. 1: Late blight on foliage of potato caused by *Phytophthora infestans.*

Fig. 2: Late blight on potato tuber caused by *P. infestans.*

Fig. 3: Late blight on potato stem, natural incidence without fungicide application.

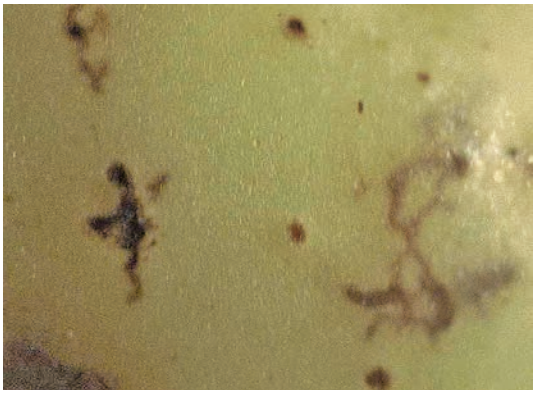

Fig. 4: Infection of a tuber via lenticels.

Fig. 5: Infection with *P. infestans* through an eye, ten days after inoculation.

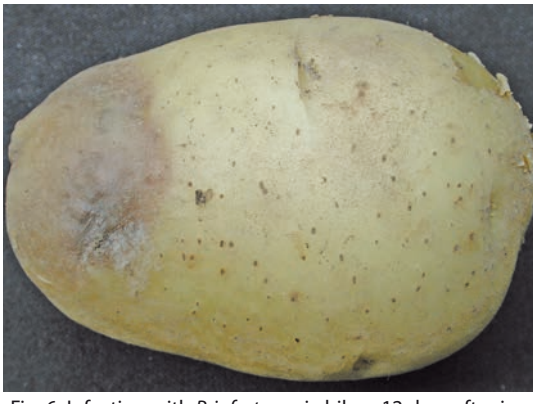

Fig. 6: Infection with *P. infestans* via hilum 12 days after inoculation.

Fig. 7: Assessment of tuber blight resistance by dipping whole tubers in suspension a day after harvest. Example of high resistance to mycelial spread.

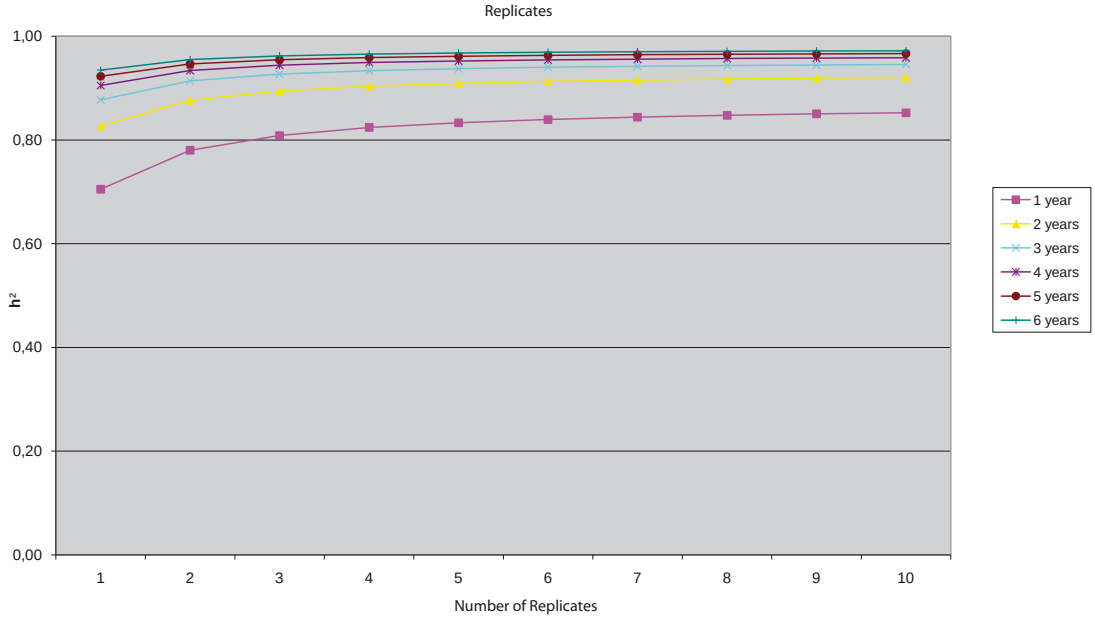

Fig. 8: Simulated relative heritabilities (h^2) of final AUDPC values for varying numbers of replicated plots per year calculated using formula: h2 = genetic variance component / [genetic variance component + (genotype-year interaction variance component / number of years) + (residual variance component/ [number of years x number of replicates])] from 854 genotypes tested three years with two replications of four plants per plot, artificially inoculated, irrigated as required, sheltered from wind, 16-18 scoring dates per year, Truberg et al. (2010).

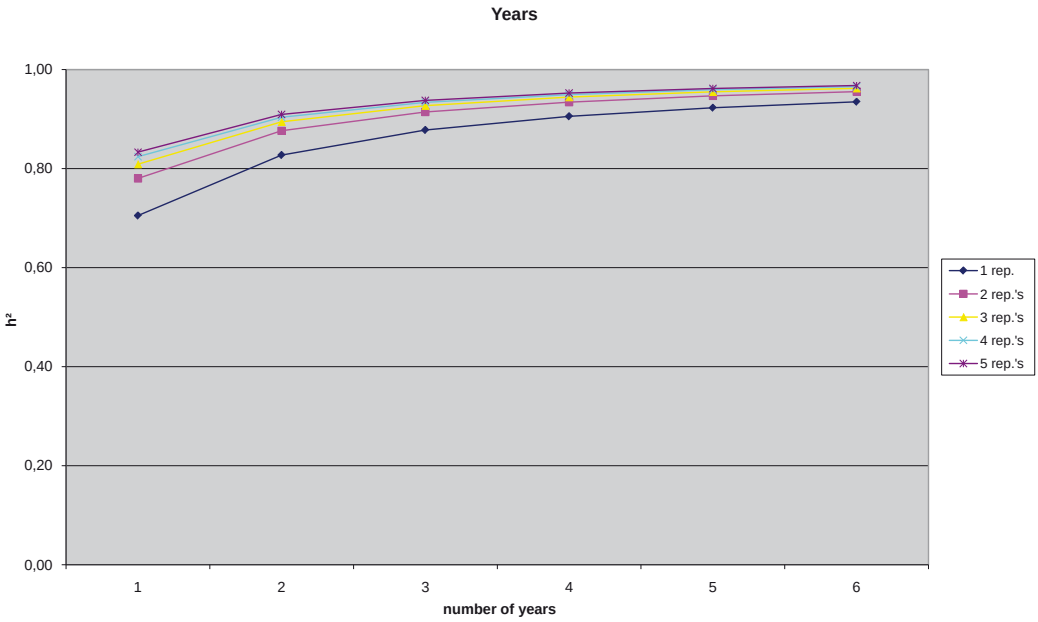

Fig. 9: Simulated relative heritabilities h^2 of final AUDPC values for varying numbers of years tested, calculated as described for Fig. 8.

Fig. 10: Assessment of foliage blight resistance on plantlets in vitro, fusionates of *blb* + *tbr*, five days after inoculation on the right, untreated on the left side.

Fig. 11: Seedlings six days after inoculation with *P. infestans*. High susceptible population on the left, quantitative high resistant one on the right, before selection.

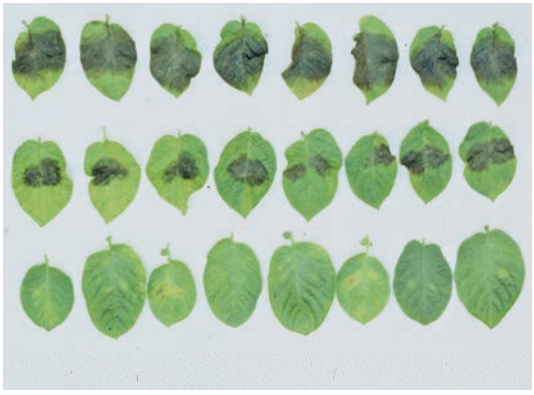

Fig. 12: Assessment on detached leaflets. Each row one clone. On the top score 2, the middle clone score 5, and below score 8.4.

Fig. 13: Necroses on hair basic of a leaf, score 8 for blemish; clone BAZ-GL-93.7024.52.

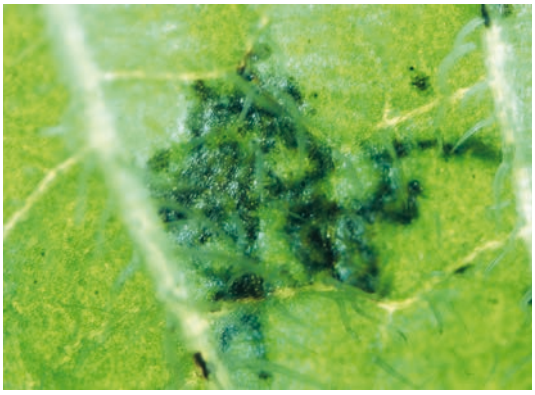

Fig. 14: Necrotic reaction under the inoculum drop, score 7 for blemish.

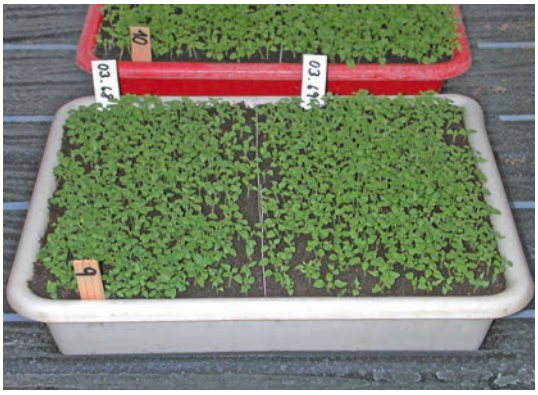

Fig. 15: Potato seedlings seven days after emerging.

Fig. 16: Planting of dihaploid seedlings about 12 days after emerging and about two weeks before inoculation with *P. infestans* suspension.

Fig. 17: Seedlings one day after selection against foliage blight susceptibility, on day of potting.

Fig. 18: Aerial mycelium of *P. infestans*, intensity 1.

Fig. 19: Lesion six days after drop inoculation, score 5.

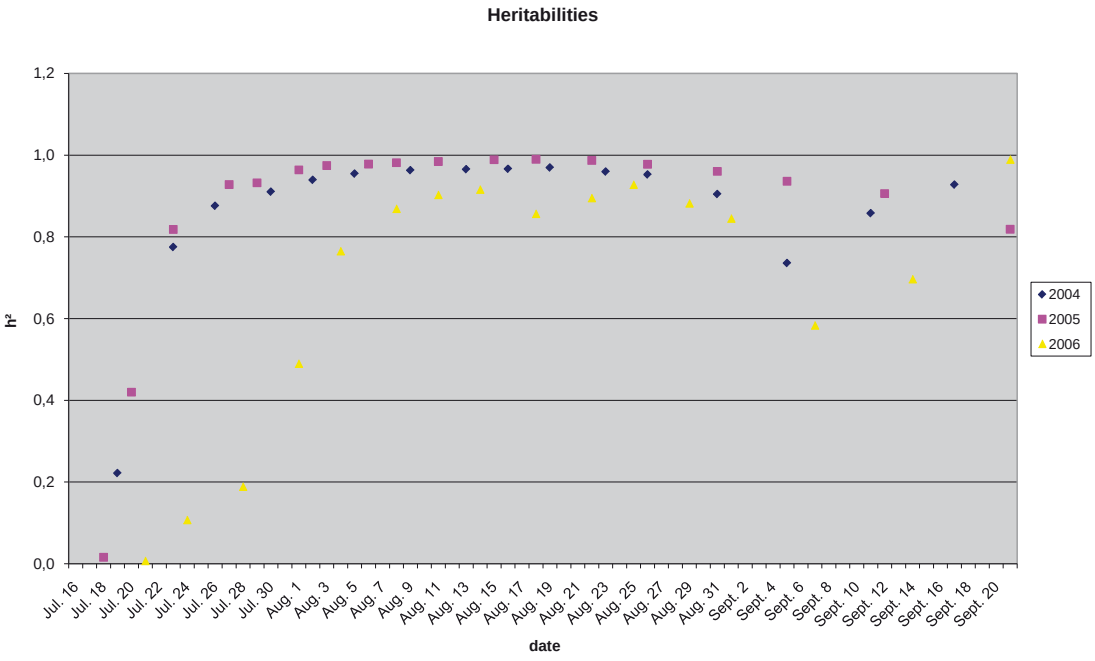

Fig. 20: Relative heritabilities (h^2) of percent foliage blight severity at single scoring dates in three successive years in average of 854 genotypes with two replicated plots in three years (Truberg et al. 2010).

Fig. 21: Assessment of quantitative foliage blight resistance in an isolated field with irrigation, inoculation and shelter from wind. Photo on August 9 2004.

Fig. 22: Field assessment of foliage blight resistance. Maturing with little late blight spots is desired as in the centre. Photo on August 14 2001.

Fig. 23: Late blight resistant dihaploid clone BAZ-GL-86.082.01 P St Eca with resistance of foliage to spread and sporulation.

Fig. 24: Late blight on potato stem and petioles sporulating, incidence on *S. phureja* x *S. tuberosum* ssp. *tuberosum* without fungicide application; stem infection occurred long time before leave infections.

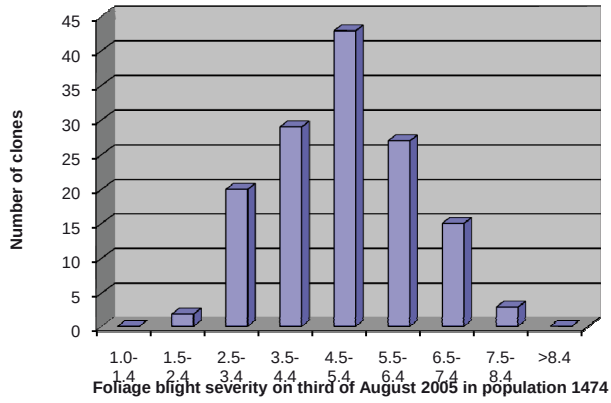

Fig. 25: Foliage blight on the dihaploid population 1474 on August 03, 2005. For severity scale of disease see table 16. Parents and its foliage blight and maturity: BAZ-GL-94.7171.62 (8.1, 3.1), PD163 (6.3, 1.8).

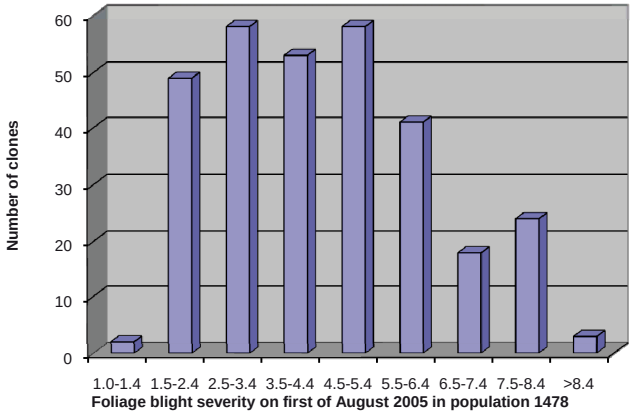

Fig. 26: Foliage blight on the tetraploid population 1478 on August 01, 2005. For severity scale of disease see table 16. Parents and its foliage blight and maturity: BAZ-GL-93.7015.04 (6.3, 5.1), Delikat (2.6, 6.3).

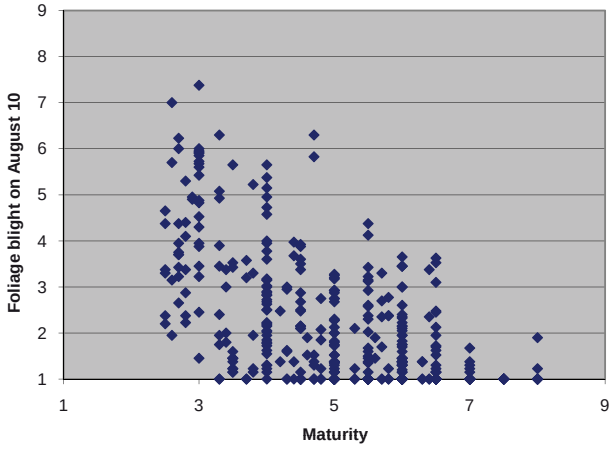

Fig. 27: Foliage blight severity and maturity of the tetraploid population 1475 on August 10, 2004. Parents and its foliage blight and maturity: BAZ-GL-94.7082.15 (4.3, 5.0), Delikat (2.2, 6.3).

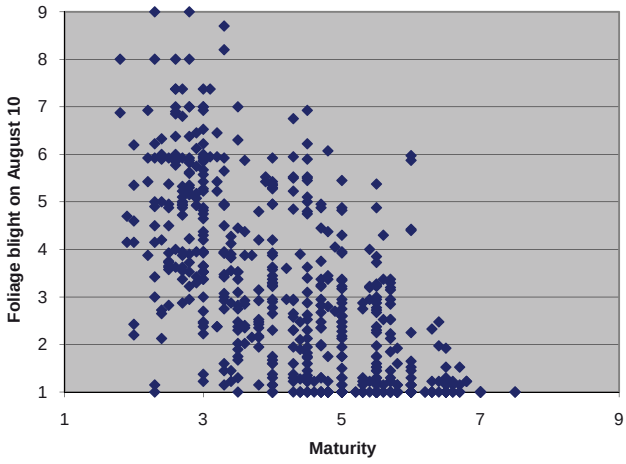

Fig. 28: Foliage blight severity and maturity of the tetraploid population 1478 on August 10, 2004. Parents and its foliage blight and maturity: BAZ-GL-93.7015.04 (4.1, 5.1), Delikat (2.2, 6.3).

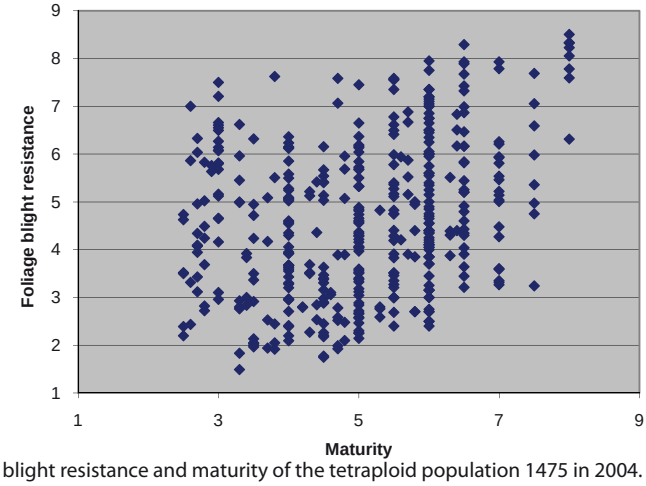

Fig. 29: Foliage blight resistance and maturity of the tetraploid population 1475 in 2004. Parents and its resistance and maturity: BAZ-GL-94.7082.15 (7.6, 5.0), Delikat (2.6, 6.3).

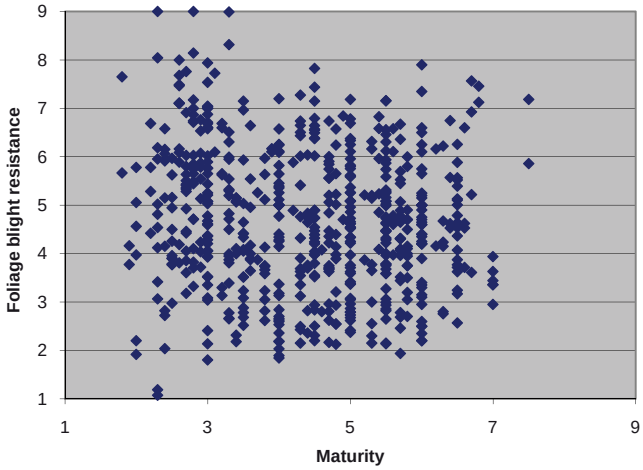

Fig. 30: Foliage blight resistance and maturity of the tetraploid population 1478 in 2004. Parents and its resistance and maturity: BAZ-GL-93.7015.04 (8.6, 5.1), Delikat (2.6, 6.3).

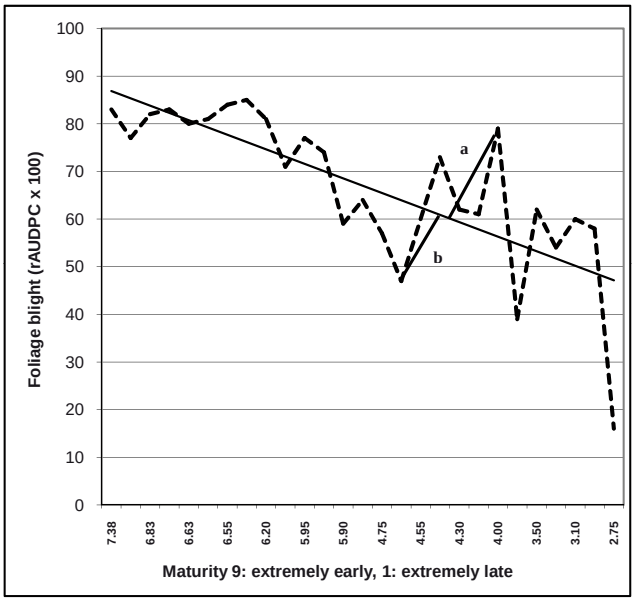

Fig. 31: Foliage blight of 27 cultivars as relative area under disease progress curve (rAUDPC x 100) and its regression to maturity. Vertical distance a to regression line is the measure of resistance of a susceptible clone (positive value), distance b of a resistant one (negative value).

Fig. 32: Assessment of tuber blight resistance of seedlings on little tubers grown in pots in greenhouse. Cutting and inoculation by dipping in suspension of *P. infestans*.

Fig. 33: Assessment of tuber blight resistance of seedlings on little tubers grown in pots in greenhouse. Estimation of disease level seven days after inoculation.

Fig. 34: Assessment of tuber blight resistance of seedlings on little tubers grown in pots in greenhouse. Examples for aerial mycelium development after six days, from the left: score 3, 6, 5, and 5.

Fig. 35: Assessment of tuber blight resistance of seedlings on little tubers grown in pots in greenhouse. Examples for browning of tissue after six days, from the left: score: 7, 6, and 4.

Fig. 36: Assessment of tuber blight resistance by tuber slice test. Examples showing different level of resistance (1, 8.5, 2 from above) as well as clone-specific expression of aerial mycelium and browning six days after inoculation. Each row one clone.

Fig. 37: Assessment of tuber blight resistance by dipping whole tubers in suspension a day after harvest. Each bag holds one clone.

Fig. 38: Assessment of tuber blight resistance by dipping whole tubers in suspension a day after harvest. Result of cultivar Resy 12 days after inoculation on the second observation date. All tubers remained after first observation are blighted now.

Fig. 39: Assessment of tuber blight resistance by dipping whole tubers in suspension a day after harvest. Result of two BC4 clones 28 days after inoculation. Number 118 is completely rotten (BAZ-GL-99.8089.05, score 2), number 188 is highly quantitatively resistant (BAZ-GL-FH 98.04.11, score 8.5).

Fig. 40: Blue bruise in four late blight resistant clones estimated with score 4 and 1 at upper left and right, respectively, score 7 and 6 at the bottom left and right.

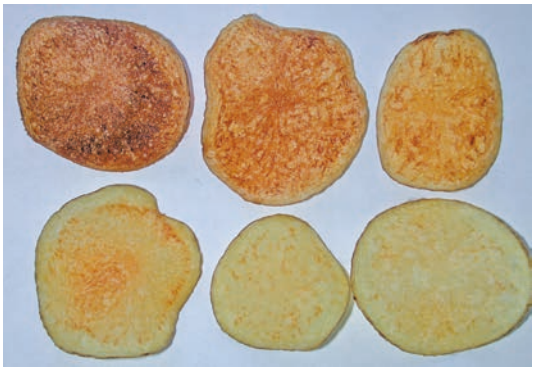

Fig. 41: Estimation of colour of crisps in scores from upper left to bottom right: 3, 4, 5, 6.5, 8, and 8.5 in the 1-9 scale.

Fig. 42: Rods are rinsed with running water and then wiped.

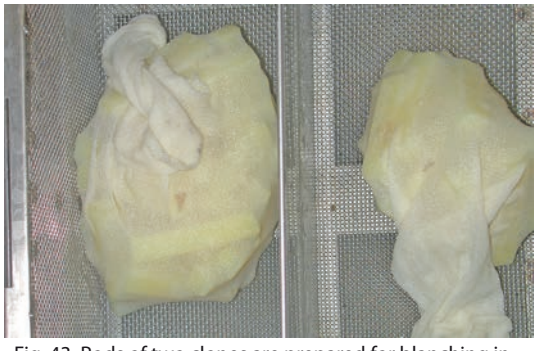

Fig. 43: Rods of two clones are prepared for blanching in water.

Fig. 44: Sample of four clones drip off before frying in fat.

Fig. 45: Consistency of cooked tubers is estimated by using a fork.

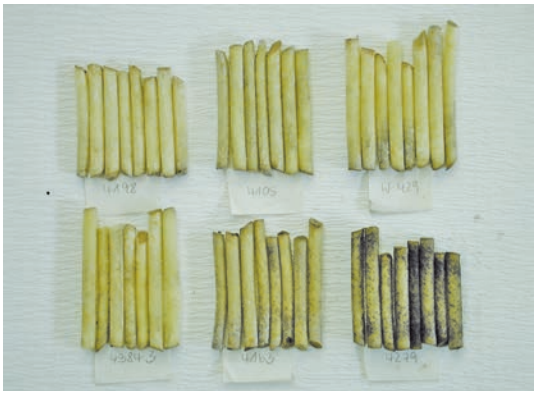

Fig. 46: Assessment of row tuber tissue discolouration. Observation 18 hours after core out of two cylinder bores of each of four tubers with a cork-drill. Scores 7, 5, and 6, are given from upper left to right for Pirol, Agria, BAZ-GL-01.1571.02, and bottom left to right score 4, 3, 1 for BAZ-GL-01.1462.01, BAZ-GL-01.1572.08 and BAZ-GL-01.1512.03, respectively.

Fig. 47: Potato plant with typical symptoms of leaf roll disease caused by PLRV-infection.

Fig. 48: Excised-bud assay for estimation of virus infections in seed potatoes is started in January. The photo shows the design before putting into the earth.

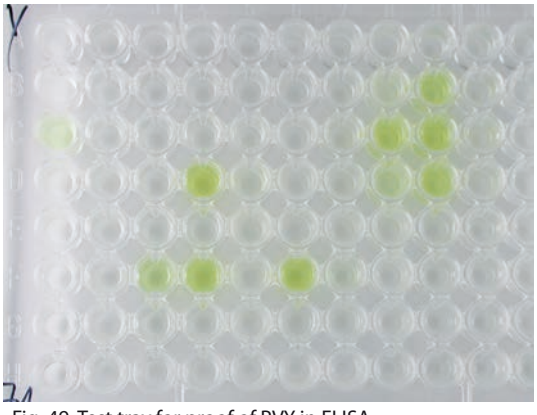

Fig. 49: Test tray for proof of PVY in ELISA.

Fig. 50: Leaflet invaded by *Alternaria* sp., small type of spots.

Fig. 51: Incidence with *Alternaria* sp., large type of spots.

Fig. 52: Incidence with *Botrytis* sp.

Fig. 53: Incidence of Sarpo Mira with *Alternaria* sp. and *Botrytis* sp.

Fig. 54: Stolones and tubers of a clone (*S. demissum* x *S. tuberosum* ssp. *tuberosum*) in the field at the end of September.

Fig. 55: Clone BAZ-GL-01.1206.17 P Sp with a bit rough skin, oval shape, and general tuber impression 7.5.

Fig. 56: Skin colour grey brown, scaly, lenticels very large (1).

Fig. 57: Skin condition: netted.

Fig. 58: Clone BAZ-GL-00.1106.04 P Sp Ch Po Kr1 Ro1 with rough skin, oval to long oval (see table 46 and pedigree 8.4.).

Fig. 59: Skin condition: a bit rough on the left, smooth on the right.

Fig. 60: Skin ochre, very smooth, lenticel size middle (score 5) and score 6.5 for lenticel number.

Fig. 61: Example for pear-shaped tuber, large size of lenticels (score 2), number of lenticels: score 4.

Fig. 62: Prominent hilum.

Fig. 63: Late blight resistant clone BAZ-GL-99.8030.05 P (Sp) Ro1, very smooth skin, good tuber blight resistance.

Fig. 64: Tubers of clone BAZ-GL-01.1332.02 P Pa2 Pa3 St Ro1 from ((*dms* x sto) x Kardent).

Fig. 65: Clone BAZ-GL-01.1336.01 P Ro1, a BC2 from *blb*. Nice and resistant to late blight, but without economical value.

Fig. 66: Clone BAZ-GL-00.1206.05 P Sp with smooth skin, round oval to oval shape, shape crossways: score 8.5, se-sl..

Fig. 67: Skin ochre, a bit rough, lenticels very large (1) and frequently (3).

Fig. 68: Scale for estimation of dormancy from upper left (score 9) to bottom right (score 2).

Fig. 69: Example of internal rust spot.

Fig. 70: Intense incidence of tuber scab (score 2) on cultivar Champion, Ireland 1995.

Fig. 71: *Solanum demissum*.

Fig. 72: Changing of tuber size, shape, stolon development and eye depth from wild species (on the left) to backcross four by breeding in the order F1 (second figure from the left, *dms* x *tbr*), BC2, BC3, BC4 (two tubers each) from the following generations.

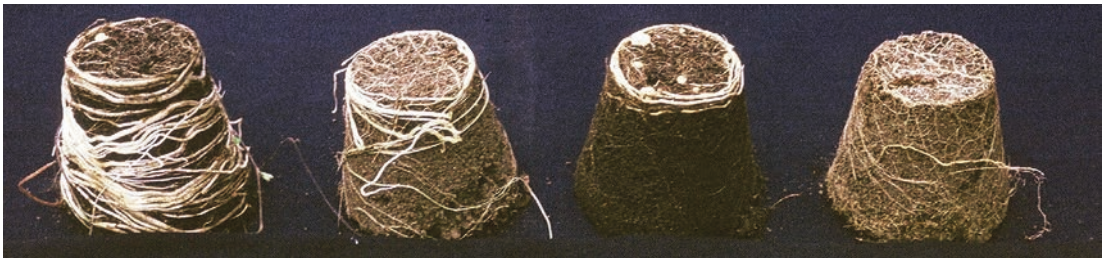

Fig. 73: Genotypic variation in stolon development between clones of *S. pinnatisectum*.

Fig. 74: Tubers of *S. demissum* (part of a Petri dish with ø 10 cm).

Fig. 75: Tuber size of wild (on the left) in proportion to cultural potato (on the right).

Fig. 76: Crossing, break away the stamen from the flower two days before pollination of the remaining female part of the flowers.

Fig. 77: Development of berries, 7 days after pollination.

Fig. 78: Growing and maturing of berries in a bag, 6 weeks after pollination.

Fig. 79: Clone BAZ-GL-96.7036.03, BC1, ([(*S. demissum* x *S. stoloniferum*) x cultivar] x GL-VI-82.9269.10), photo on 04.08. 2001.

Fig. 80: Variation in skin colour and tuber shape in a progeny ((*dms* x *sto*) x *tbr*).

Fig. 82: Hybrid *Solanum demissum* x *S. stoloniferum*.

Fig. 81: High male and female fertility causes visible development of berries few days after flowering; so an inflorescence can have berries and flowers at the same time.

Fig. 83: Wild potato clones in the field. Clone BAZ-GL-93.7024.59 on the left (*dms* x *sto*), BAZ-GL-85.6257.08 on the right side (*ver* x *dms*). Cultivar Adretta in the foreground. Photo on August 04, 2001.

Fig. 84: Selected clone of *dms* on the left, hybrid ((*dms* x *tbr*) x *tbr*) on the right.

Fig. 85: A-Clones with high part of 'wild' genes, each row a clone, photo on June 22, 2002. From left: F1 (*dms* x *sto*) x *tbr*, F1 ((*dms* x *adg*) x *tbr*), ((*pta* x *tbr*) x *tbr*).

Fig. 86: Late blight resistant BC2-clone from *pta*. Photo on August 08, 2005.

Fig. 87: A tetraploid clone from fusion of diploid *blb* with dihaploid *tbr*, grown in the field. Photo on September 10, 1997.

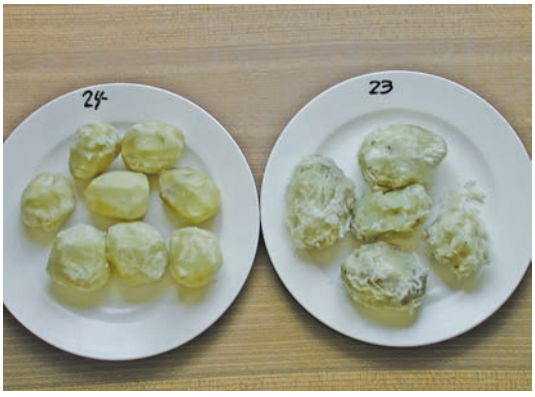

Fig. 88: Assessment of suitability for table potato: Examples of two BC2 clones with appearance after cooking score 2 (number 24) and 1 (number 23), disintegration on cooking score 3.5 (number 24) and 2.5 (number 23), respectively.

Fig. 89: On the left *blb*, on the right *pnt*, in between (*blb* x *pnt*).

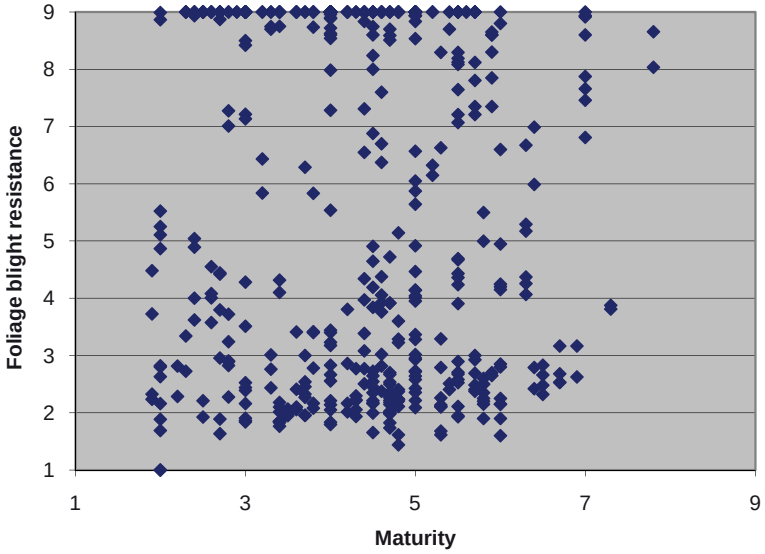

Fig. 90: Foliage blight resistance and maturity of the tetraploid population 1476 in 2004. Frequency contribution of resistance supported assuming partly R-gene-effect. Parents with its (resistance, maturity) are BAZ-GL-Tue-98.02.13 (8.7, 2.9) and Leyla (2.5, 7.7).

Fig. 91: Early late blight resistant clone BAZ-GL-00.1218.01 P Sp Kr1 Ro1, BC3 from *crc* on the left side. Photo on August 03, 2004 in field assessment of foliage blight resistance.

Fig. 92: Clone BAZ-GL-00.1218.01 P Sp Kr1 Ro1, BC3 from *S. circaeifolium*.

Fig. 93: Cultivation of potato seedlings, about 8-9 days after sowing the seeds.

Fig. 94: Planting of material for field assessment on foliage blight resistance.

Fig. 95: Breeding garden, part potato of ZL Gross Luesewitz 2002.

Fig. 96: Group 1 (4x P ese), very early to second early maturing *Phytophthora*-resistant clones, photo on August 08, 2002.

Fig. 97: The range of maturity in late blight resistant pre-breeding material. Photo on August 04, 2001.

Fig. 98: Maturity in late blight resistant pre-breeding A-clones has a considerable second-early and early part. Photo on August 04, 2001.

Fig. 99: Second early late blight resistant clone BAZ-GL-94.7082.15 P Sp Po Kr1 Kr18 V. Photo on August 14, 2002 in field assessment of foliage blight resistance.

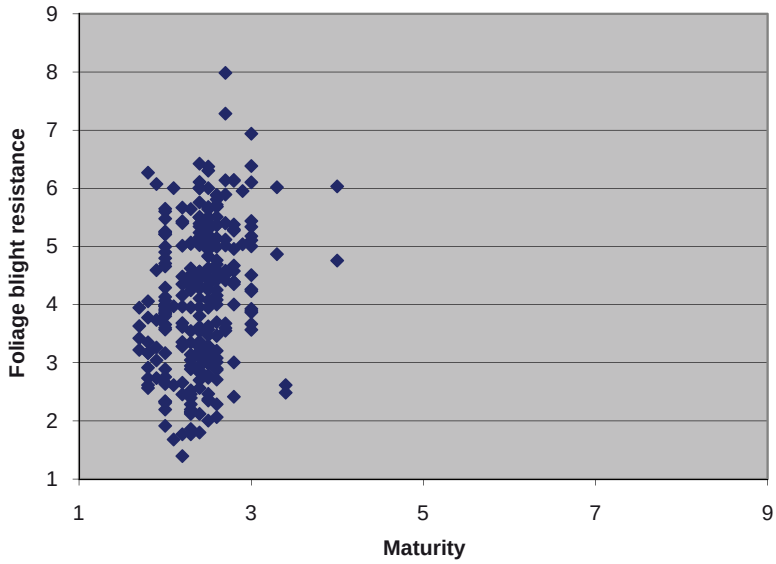

Fig. 100: Foliage blight resistance and maturity of the dihaploid population 1474 in 2004. Parents and its (resistance and maturity): BAZ-GL-94.7171.62 (7.0, 3.1), PD163 (2.8, 1.8).

Fig. 101: *Phytophthora*-resistant clone suitable for French fries, BAZ-GL-00.1004.02 P Sp Po.

Fig. 102: Clone BAZ-GL-01.1555.13, resistant to late blight, Ro1 and Pa2, suitable for French fries and table potato.

Fig. 103: Clone BAZ-GL-00.1106.05 P Sp Ch, *Phytophthora*-resistant, suitable for crisps and table potato with very rough skin, descendant from Tessi.

Fig. 104: Range of discolouration in crisps production of late blight resistant pre-breeding material with scores 6.5, 4, 1.5, 3, 7, 5 from upper left to bottom right.

Fig. 105: Clone BAZ-GL-01.1293.01 P St Po Kr1 with netted skin, long.

Fig. 106: Clone BAZ-GL-02.5029.13 P Sp (St) Po Ro1 with a bit rough skin, oval. See pedigrees 8.

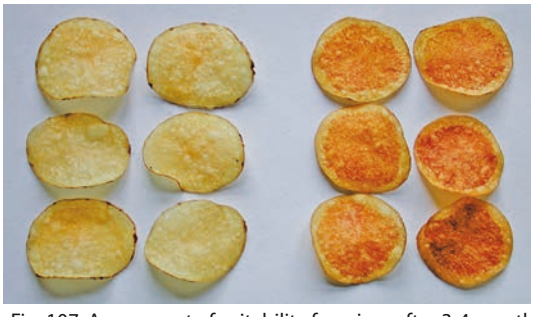

Fig. 107: Assessment of suitability for crisps after 3-4 month storage at 4°C. Score 7 was given the clone with desired expression on the left side (BAZ-GL-03.5059.05 P St Ch Po Kr1 Ro1), score 5 on the right (BAZ-GL-03.5118.09 P (Sp) Ro1) as too discoloured.

Fig. 108: Clone BAZ-GL-00.1106.05 P (Sp) Ch Po Ro1 with a bit rough skin, oval, a descendant of Tessi.

Fig. 109: Clone BAZ-GL-02.1412.02 P Sp Po with a bit rough skin, oval. See pedigrees 9.

Fig. 110: Clone BAZ-GL-01.1577.06 P (Ch) Po Ro1 with smooth skin, oval.

Fig. 111: Clone BAZ-GL-01.1272.03 P Sp St Po Ro1 with smooth skin, oval, a hybrid of Panda x BAZ-GL-94.7237.05.

Fig. 112: Assessment of suitability for French fries. On the left side unsuitable examples because of discolouration by frying, above BAZ-GL-02.5028.15 P Sp Kr1 Ro1 (score 2.7), below BAZ-GL-03.5119.01 P Sp Tt Kr1 Ro1 (see pedigree 6, score 4). On the right: above BAZ-GL-02.5029.23 P Sp Po (see pedigrees 8, score 6.5) and below BAZ-GL-03.5059.05 P Sp Po (see pedigrees 8, score 8).

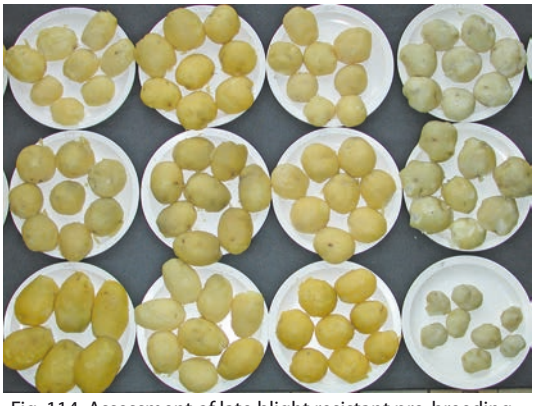

Fig. 114: Assessment of late blight resistant pre-breeding material for discolouration after cooking, part of clones.

Fig. 113: Clone BAZ-GL-00.1218.01 P Sp Kr1 Ro1 with good appearance after cooking, nearly no disintegration during cooking, firm consistency, a bit mealy and taste middle.

Fig. 115: Tubers of clone BAZ-GL-00.1186.04 P Sp Kr1 Eca after assessment of resistance to blue bruise (score 8). The clone is highly resistant to *P. infestans* and, suitable for table potato.

Fig. 116: Tubers of clone BAZ-GL-01.1467.01 P (Sp Ch) Ro1, a BC2 from *S. okadae*.

Fig. 117: Clone BAZ-GL-99.8084.01 P Sp Ro1, mealy, with a bit rough skin, round-oval, handed over to variety breeders in 2006. See pedigree 9.6.

Fig. 121: Clone BAZ-GL-00.1076.10, early to second early, high starch content, resistant to Pa2 and Pa3.

Fig. 118: Tubers of clone BAZ-GL-95.7286.01 P St (Po) Eca ten days before planting, handed over to variety breeders 2002. See table 50.

Fig. 119: Tubers of clone BAZ-GL-94.7235.03 P St Po Kr1 Pe ten days before planting, handed over to variety breeders 2002. See table 50.

Fig. 120: Tubers of clone BAZ-GL-93.6984.07 P St ten days before planting, handed over to variety breeders 2002. See table 50.

Fig. 122: Clone BAZ-GL-01.1569.02 P Pa2 Pa3 St Ch Kr1with a bit rough skin, oval shape. Descendant from Kartel. See table 46 and 51.

Fig. 123: Clone BAZ-GL-00.1079.05 P St Pa2 Pa3 Ro1 Ro2 Ro3 Ro5 Kr1 with very rough skin, round.

Fig. 124: Tubers of clone BAZ-GL-01.1571.05 P Pa2 Pa3 Sp, a BC2 from *S. okadae*.

Fig. 125: BC2-clones resistant to late blight and *G. pallida*. From left: BAZ-GL-01.1572.03 P Pa2 Pa3 from *oka*, BAZ-GL-01.1572.02 P Pa2 from *oka*, BAZ-GL-01.1446.01 P Pa2 Pa3 from *dms*. Photo on August 24, 2005 in field assessment of foliage blight resistance.

Fig. 126: Dihaploid clones highly resistant to *Globodera pallida* Pa2 and Pa3.

Fig. 127: Clone BAZ-GL-98.236.01 P Sp Ro1 Ro2 Ro3 Ro5 with netted skin, oval.

Fig. 128: Clone BAZ-GL-00.1143.07 P Sp Ro1 with high late blight resistance on foliage and tubers and shallow to very shallow eye depth (score 8).

Fig. 129: Tubers of dihaploid clone BAZ-GL-97.169.01 Sp Ch Po in assessment of blue bruise (score 7.2), colour of tuber flesh 7.

Fig. 130: *Phytophthora*-resistant dihaploids in breeding garden 2002.

Fig. 131: Dihaploid clone BAZ-GL-01.1483.08, suitable for French fries and table potato, resistant to *P. infestans*, Pa2 and Ro1.

Fig. 132: Dihaploid clone BAZ-GL-97.7006.01 P (Ch) V Kr1 Kr18, maturing early with rare and very late little foliage blight spots in the special late blight field assessment.

Fig. 133: Late blight resistant dihaploid clones, early to second early. From left: BAZ-GL-93.6997.07 P (St Po) Kr1 Kr18 Pe, BAZ-GL-96.6997.01 P St (Sp), BAZ-GL-96.6991.37 P (Sp) Kr1 Kr18 V, photo on August 13, 2001 in field assessment of foliage blight resistance.

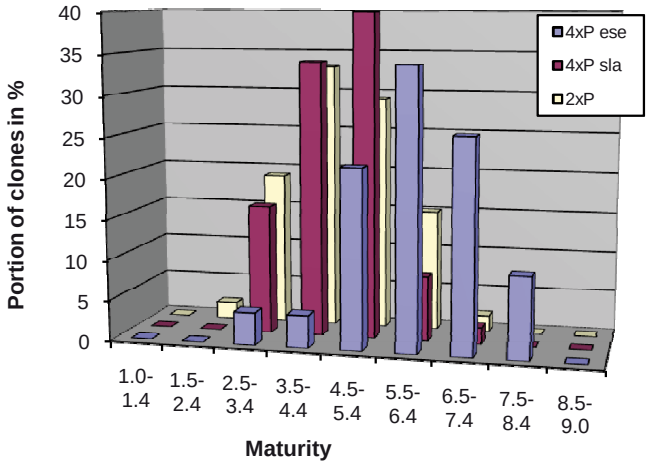

Fig. 134: Maturity of late blight resistant pre-breeding material in assessment of the year 2006, result of all tested B- to D-clones. Frequency distribution of three groups in classes of maturity according to yellowing of the haulm.

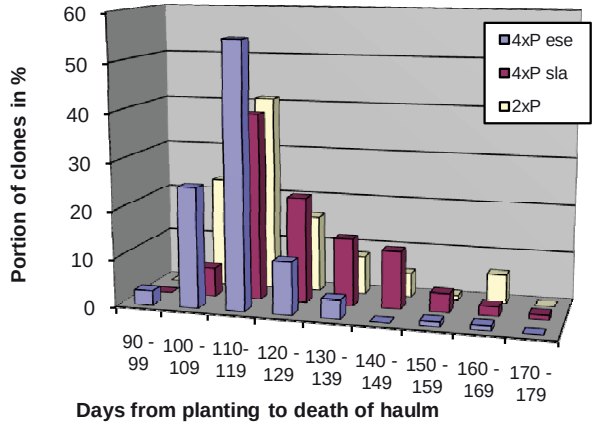

Fig. 135: Maturity of late blight resistant B- to D-clones 2006 estimated according to duration of number of days from planting to dying of haulm.

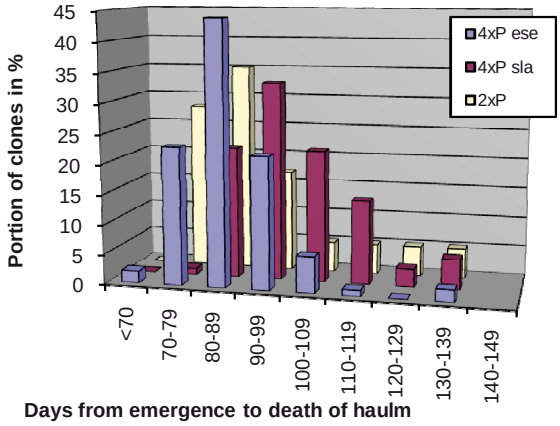

Fig. 136: Maturity of late blight resistant B- to D-clones 2006 estimated according to duration of number of days from emergence to dying of haulm.

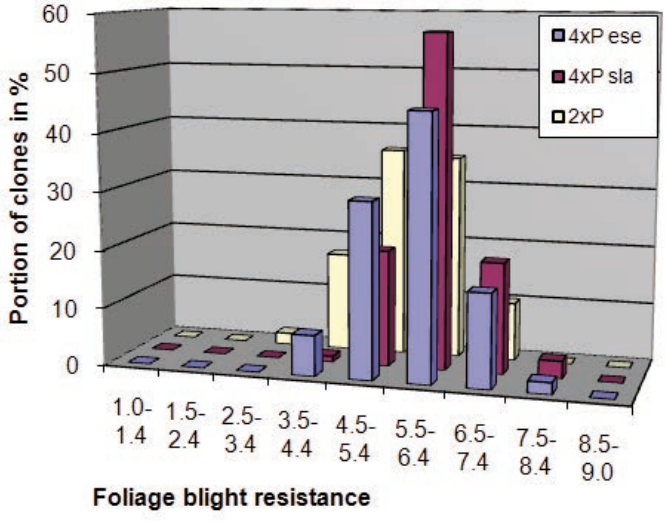

Fig. 137: Frequency distribution of results of foliage blight resistance of B- to D-pre-breeding clones of ZL in field assessment 2006.

Fig. 138: Potato leaflet attacked by *Alternaria* sp. und *Botrytis* sp.

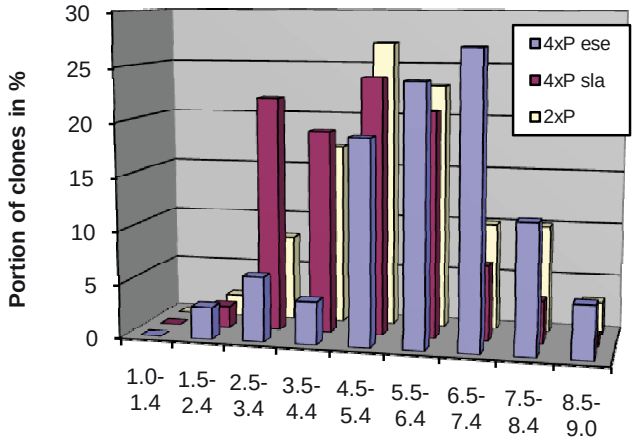

Fig. 139: Frequency distribution of severity of attack of potato foliage by *Alternaria* sp. and Botrytis sp. in late blight resistant pre-breeding material of ZL in the field 2006. Score 9 means free of disease; score 1 highest severity of the disease.

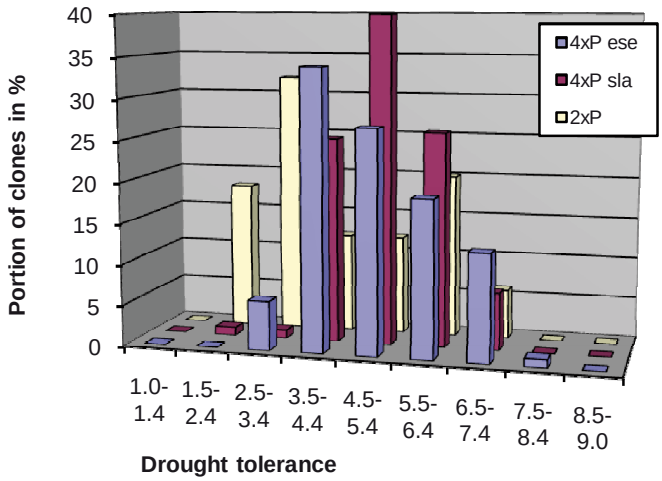

Fig. 140: Drought tolerance in late blight resistant pre-breeding material of ZL in the field 2006. Score 9 means no reaction, score 1 highest depression.

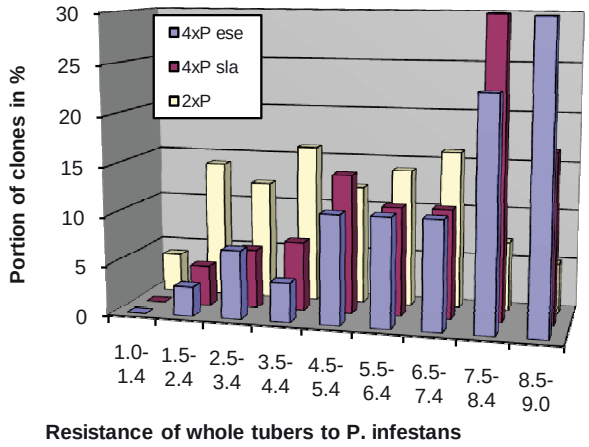

Fig. 141: Frequency distribution of tuber blight resistance in late blight resistant pre-breeding material of ZL in 2006. Assessment of whole tubers with inoculation one day after harvest.

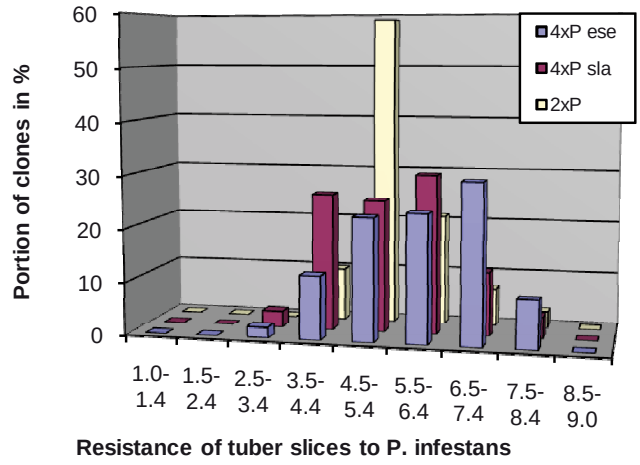

Fig. 142: Frequency distribution of tuber blight resistance in late blight resistant pre-breeding material of ZL in 2006. Assessment of tuber slices in December.

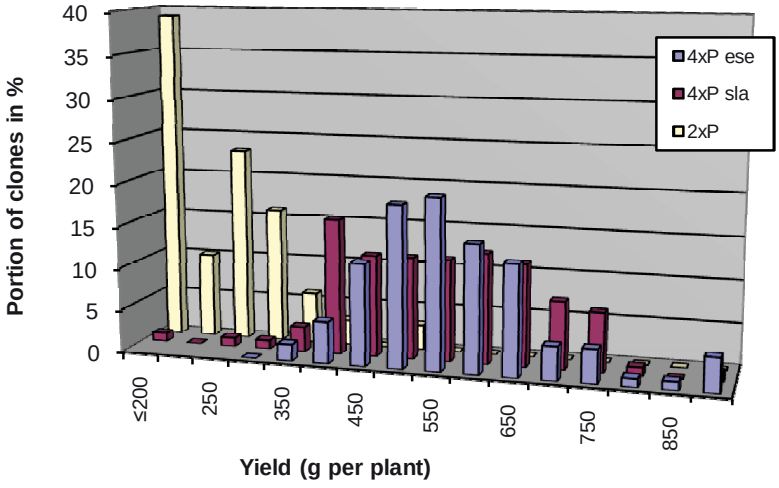

Fig. 143: Frequency distribution of tuber yield in late blight resistant pre-breeding material of ZL in 2006.

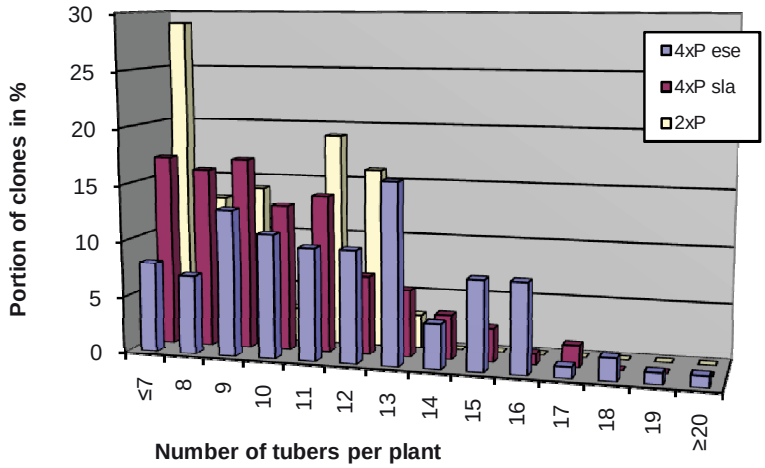

Fig. 144: Frequency distribution of tuber number in late blight resistant pre-breeding material of ZL in 2006.

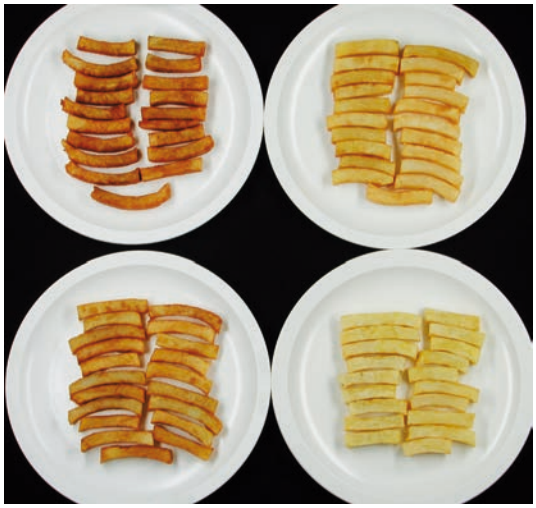

Fig. 145: Four late blight resistant clones in assessment of suitability for French fries: BAZ-GL-02.5013.06 P Kr1 Ro1 (score 3) at upper left and BAZ-GL-01.1272.03 P Po Ro1 Ro2 Ro3 Ro5 with score 6.5 at upper right, respectively, BAZ-GL-02.5036.02 P Sp Kr1 Ro1 Ro2 Ro3 (score 4.5 at the bottom left) and BAZ-GL-02.1308.01 P St Kr1 Kr18 with score 8 for French fries colour on the right.

Fig. 146: Late blight resistant clone BAZ-GL-01.1272.03 P Sp (St) Po Ro1, tuber skin netted, a bit roughly.

Fig. 147: Late blight resistant clone BAZ-GL-00.1195.13 P St Ch, tuber skin netted, a bit roughly.

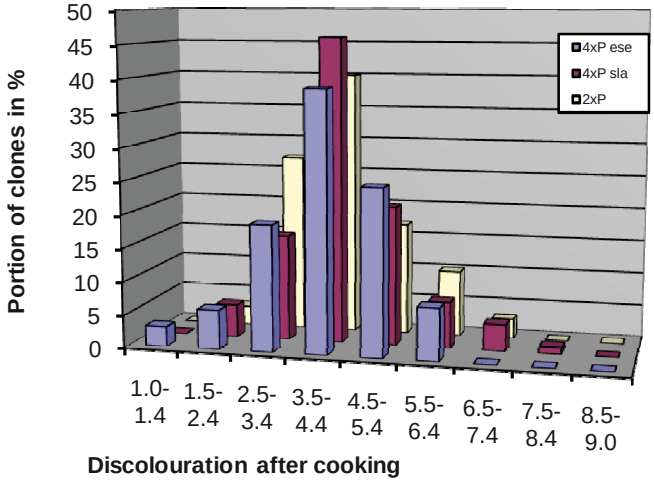

Fig. 148: Discolouration after cooking of late blight-resistant pre-breeding material in 2006.

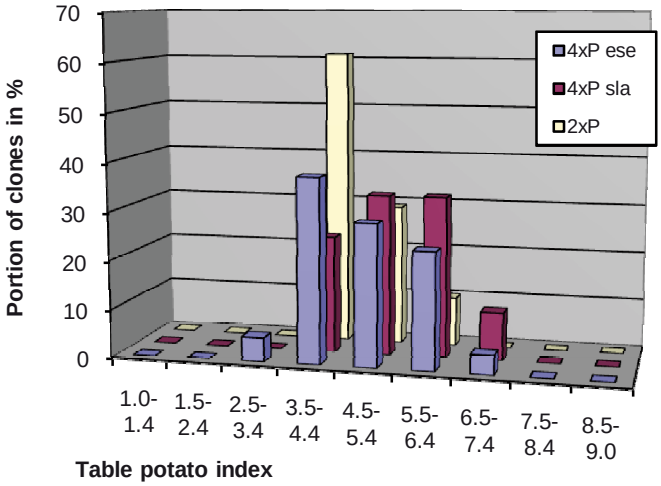

Fig. 149: Assessment of table potato index of late blight-resistant pre-breeding material of the late blight subprogram table potato in 2006.

Fig. 150: Disintegration after cooking of clone BAZ-GL-00.1185.01 P Sp with score 2.7, consistency 3.3, mealiness 2.8, and taste 4.

Fig. 151: Clone BAZ-GL-00.1143.07 P Sp Ro1 with high late blight resistance and suitability for table potato.

Fig. 152: BC3-clone from *S. stoloniferum*, highly late blight-resistant and suitable for table potato.

Fig. 153: Nice oval to long-oval late blight-resistant clone BAZ-GL-01.1396.01 P Sp Ro1 with excellent tuber blight resistance.

Fig. 154: Nice round-oval late blight-resistant clone BAZ-GL-99.8084.01 P Sp (St) Ro1 with smooth skin.

Fig. 155: Discolouration of row tuber flesh after 24 hours of clone BAZ-GL-01.1395.01 P Sp on the left (Score 4.7, see pedigrees 9) and of BAZ-GL-02.5029.13 P Sp Po Ro1 (score 6.8, see pedigrees 8) on the right side in 2006.

Fig. 156: Variation in assessment of resistance against blue bruise in pre-breeding material for *Phytophthora*-resistance.

Fig. 157: Exposition of late blight resistant pre-breeding potato clones at Agricultural Exhibition, June 24-27, 2004 at Dummerstorf, Germany.

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Vorlaufzüchtung und Sortenzüchtung der Kartoffel auf quantitative Resistenz gegen *Phytophthora infestans* an Kraut und Knollen und für verschiedene Nutzung – Probleme, Lösungen und Ergebnisse.

In der langen Geschichte der *Phytophthora*-Resistenzzüchtung der Kartoffel erwies sich die quantitative Resistenz als schwierig sowohl hinsichtlich der Merkmalserfassung als auch des Zuchtfortschritts bei polygener Vererbung und dem sehr langen Zuchtweg durch Nutzung von Wildarten als Resistenzquelle. Gegenüber der R-Gen-Resistenz hat sie jedoch lang anhaltende Wirkungsdauer. Der Intensität züchterischer Bemühungen und ihrem Fortschritt unter Langtagbedingungen standen methodische und ökonomische Gründe entgegen; chemische Bekämpfung stellte die einfache Lösung dar, deren Aufwand um ein Drittel durch Züchtung gesenkt werden könnte.

Mehr als 40-jährige Vorlaufzüchtung im ZL Groß Lüsewitz führte zu methodischen Entwicklungen und Zuchtergebnissen, die eine Korrektur sowohl des Werts quantitativer Resistenz als auch der Erfolgsaussichten für die Kombination mit anderen quantitativen Merkmalen erfordert sowie der meisten bisherigen molekulargenetischen Interpretationen. 74 Tabellen, 157 Abbildungen und 33 Stammbäume geben Einblick in methodische Details und Zuchtergebnisse für 68 Merkmale. Prüfungsmethodische und züchterische Problemlösungen werden erläutert. Langsamer Zuchtfortschritt war bei Kombination von Resistenz mit anderen quantitativen Merkmalen zu verzeichnen. Auf nötige Änderungen im Selektionssystem der Sortenzüchtung zur Nutzung quantitativer Resistenz gegen *P. infestans* wird hingewiesen. Der Stand der Forschung zur Pathogenität von *P. infestans* und zur Resistenz wird analysiert sowie der internationale Stand der quantitativen *Phytophthora*-Resistenz von Sorten, der Ursachen unzureichender Resistenz und heutige Erfolgsaussichten. Charakterisierung und Wertung von Prüfungsmethoden an Kraut und Knollen, Erblichkeit behandelter Merkmale, Untersuchung und Nutzung von Wildarten sind umfangreich berücksichtigt. Alte und meist ignorierte Literatur ist einbezogen. An die Sortenzüchtung abgegebenes Zuchtmaterial wurde in wichtigen Merkmalen beschrieben und lässt den Zuchtfortschritt über 30 Jahre erkennen. Schlussfolgerungen für zukünftige Nutzung quantitativer *Phytophthora*-Resistenz werden gegeben sowie Empfehlungen für die Durchführung dieser Vorlaufzüchtung in der EU.

Pre-breeding and breeding of potatoes for quantitative resistance to *Phytophthora infestans* on foliage and tubers and for different utilization - problems, solutions and results.

During the long history of breeding for late blight resistance of the potato the quantitative type of resistance became apparent to be very difficult not only concerning the assessment of the both traits but also concerning breeding progress because of polygenic inheritance and the very long breeding way from wild species as source of resistance. Compared with R-genes this type has the advantage of lastingness. However methodical and economical arguments were opposed to breeding effort and progress in long-day conditions; chemical plant protection was the alternative; its application could be reduced by one third by breeding for resistance.

Pre-breeding for more than 40 years at ZL Gross Luesewitz resulted in development of methods and breeding material which requires revision as well of value of quantitative type of blight resistance as chance of success to combine resistance with other quantitative traits, and of most interpretations of molecular genetic results. 74 tables, 157 figures and 33 pedigrees inform about methodical details and results of breeding in 68 traits. Solution of problems in assessment of resistance and in breeding are explained. Slow breeding progress was stated in combining resistance with other quantitative traits. Necessary changing in selection system of variety breeding is recommended to improve efficiency of introduction of quantitative blight resistance. State of research of pathogenicity of *P. infestans* and of resistance is analysed, also global state of quantitative resistance in varieties, reasons of insufficient resistance level and current chances of success. A comprehensive overview is given about methods of assessment of blight resistance on foliage and tubers, on inheritance of mentioned traits, on assessment and use of wild species. The very extensive number of references includes elder and usually ignored literature. Pre-breeding material handed over to variety breeding is characterized in important traits and shows breeding progress during 30 years. Conclusions for utilization of quantitative late blight resistance in future and recommendations are given for concentrated organization of this pre-breeding in EU.

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ISBN 9783955470005
02495 >
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