

Breeding potato cultivars with tubers resistant to *Phytophthora infestans*

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Summary

Available information has been reviewed on tuber resistance to *P. infestans*, its inheritance and breeding procedures used to obtain potato cultivars superior in this character.

P. infestans is worldwide the most destructive potato pathogen. Tuber resistance is an essential component of potato resistance as this pathogen is often responsible for tuber rot in storage, and infected tubers of susceptible cultivars provide an important way for its overwintering.

In Europe many cultivars and advanced breeders selections have been obtained with tuber resistance to *P. infestans*, but in the last decades no progress is noted in the mean level of this resistance in cultivars. The expression of tuber resistance depends to a large extent on testing conditions and therefore it can be difficult to evaluate. Consequently making progress in breeding is not easy, and also cultivar assessment data from various countries sometimes differ considerably.

It is concluded from published data that it should be easier to make progress in breeding potato cultivars with resistant tubers if more attention is paid to combining the various types of resistance which are already known, and if the genetic determination of durable resistance to *P. infestans* is better understood.

Introduction

Phytophthora infestans (Mont.) de Bary, responsible for late blight of foliage and tubers, is found worldwide. It is regarded to be the most important potato pathogen (Anon., 1992), reducing yields and often causing serious tuber rot in storage. In developing countries each year the crop losses due to this pathogen are estimated at nearly \$3 billion (Anon., 1996). In the European Community chemical protection against this pathogen each year requires the use of 13,100 tons of active compounds at a cost of 140 million ECU (Schepers & Turkensteen, 1994). The costs of managing late blight alone in 1995 in the Columbia Basin in USA were estimated to be approximately \$30 million (Johnson et al., 1997). In Poland potato yield losses due to *P. infestans* in field trials in unprotected potato plots were estimated to exceed 20% (Pietkiewicz, 1991). With growing interest in organic farming, resistance to *P. infestans* is gaining importance (Wastie et al., 1991).

In the last decades considerable migrations and changes in populations of *P. infestans* were noted worldwide. New populations are sometimes reported to be more

pathogenic than old ones (Fry & Goodwin, 1997; Fry & Smart, 1999). While previously in most areas only the A1 mating type was detected, now the A2 mating type is often found. The presence of both mating types makes sexual reproduction possible and this in turn increases the chance of genetic recombination and makes it possible for the fungus to overwinter in oospores. There are reports that new populations may be more pathogenic to potato tubers (Lambert & Currier, 1997; Flier et al., 1998, 1999).

Breeding for resistance to *P. infestans* was probably the first attempt at a scientifically based potato breeding (Umaerus & Umaerus, 1994), and breeders apparently worked more on resistance to *P. infestans* than on resistance to any other potato pathogen (Howard, 1978). However, the results of these breeding efforts are generally disappointing (Ross, 1986).

In the last decade problems of potato resistance to *P. infestans* have been reviewed several times (Świeżyński, 1990a; Wastie, 1991; Umaerus & Umaerus, 1994). But in these publications little attention is paid to tuber resistance although several authors recognise that it is an essential component of potato resistance to *P. infestans* (Mastenbroek, 1966; Darsow, 1987a; Bradshaw et al., 1995).

In the present review we shall attempt to summarise available information on tuber resistance, its inheritance and breeding procedures used to obtain cultivars superior in this character. What is desired are cultivars with durable resistance, but the genetic nature of such a resistance is still poorly understood. Therefore information has been collected that might be useful in achieving progress in breeding such cultivars, although it is sometimes difficult to evaluate its importance.

It seems unavoidable to present tuber resistance in the broad context of plant resistance to this pathogen. However, molecular biology of the various aspects of potato tuber - *P. infestans* interaction is regarded as being a separate research area which will not be considered; its results are still difficult to apply in most programmes of breeding potatoes resistant to this pathogen.

Tuber resistance and the potato - *P. infestans* pathosystem

Under field conditions tubers are most likely to become infected from infected foliage. Stephan (1970) compared the relative frequency of infections during plant growth and at harvest. Depending on the year, 40–80% of infections were during plant growth. There are several reports that considerable tuber infection can occur when *P. infestans* starts to spread and when only a small proportion of the leaves are infected (Hirst et al., 1965; Ullrich, 1967; Stephan, 1970; Lapwood, 1977). The foliage quickly killed by the pathogen is less dangerous. By contrast, an increased tuber infection may be found after application of fungicides if it allows prolonged sporulation on the foliage (Fehrmann, 1963; Schwinn & Margot, 1991). Due to prolonged infection risk from partly infected foliage, tuber resistance is regarded as being particularly relevant in cultivars resistant to *P. infestans* (Wastie et al., 1991). The fungus may also spread during tuber handling (Dowley & O'Sullivan, 1991), and may cause losses in pre-cut seed, especially if it is held for several days before planting (Lambert et al., 1998; Morrow, 1998).

Very young tubers, 5 to 15 mm diameter, are resistant to infection (Darsow & Meinl, 1981). Later their resistance decreases, but rises again with advancing tuber maturity. The pathogen can enter into the tubers via lenticels, eyes, growth cracks and wounds, but it does not infect through intact periderm (Pathak & Clarke, 1987). Rainfall and low soil temperature favour tuber infection (Lapwood, 1977; Sato, 1979). The rate of resistance change with progressing tuber age and the relative importance of various ways of entering the tuber by the pathogen may differ, depending on growth conditions and cultivar. In general the resistance of lenticels increases with progressing tuber growth, but it is not necessarily so with tuber eyes (Lacey, 1967; Lapwood, 1967, 1977; Adams, 1975; Darsow & Meinl, 1981; Grinberger et al., 1995). There are reports that *P. infestans* can also enter tubers via stolons (Zeck, 1957; Walmsley-Woodward & Lewis, 1977). Cortical and medullar tissues were sometimes found to differ in reaction (Lapwood & McKee, 1961; Deahl et al., 1974). At harvest the extent of infection depends to a large extent on wound depth (Darsow & Meinl, 1981). In long-stored tubers resistance decreases (Ciešlewicz, 1967; Chalenko et al., 1980; Bhatia & Young, 1985; Pathak & Clarke, 1987; Darsow, 1988).

Tubers often express resistance with necrotic reactions and stunted pathogen growth. This is called the phenomenon of arrested lesions (Wastie, 1991). Such reactions were found also in cultivars with susceptible tubers. If very young tubers were inoculated, the pathogen remained localised in the cortical tissue (Darsow & Meinl, 1981). If tubers developing under natural infection pressure were harvested at various dates (July–September), lesions sometimes failed to develop beyond 1–2 mm necrotic threads. For example, Lapwood (1977) noted them in the susceptible cv. King Edward. Spray-inoculated whole, undamaged tubers could also sometimes react with thread-like lesions (Lapwood, 1967; Malcolmson, 1981). The frequency of such reactions was higher if the tubers were inoculated following a delay after harvest (Malcolmson, 1981).

Under normal storage conditions the pathogen can survive the winter in infected tubers (Ullrich, 1957). Blighted tubers discarded on heaps from stores and clamps may start a new late blight epidemic. Such seed tubers may also be an infection source for plants which develop from them (Ullrich, 1957; Hirst & Stedman, 1960; Boyd, 1980; Zwankhuizen & Frinking, 1996). Van der Zaag (1959) found that infected seed tubers of cultivars susceptible to *P. infestans* were much more likely to produce infected stems than infected tubers of resistant cultivars.

P. infestans is unable to survive the winter as a saprophyte (Fehrmann, 1963). At present, as both mating types of the pathogen have spread into many areas, overwintering in tubers and overwintering by means of oospores are both possible. However, overwintering in tubers appears to be prevalent (Fry & Goodwin, 1997; Anderson et al., 1998; Flier et al., 1998; Hanson & Shattock, 1998; Lebreton et al., 1998).

Types of tuber resistance found in the potato

Various types of tuber resistance have been described. Potato genotypes may differ in the period when the tuber resistance is expressed and in the duration of this period. Lapwood (1967) noticed that at consecutive harvests of resistant cultivars, resistance

increased quickly while in susceptible ones there was no progress in resistance. Depending on cultivar the resistance could be expressed more in lenticels or more in eyes (Walmsey-Woodward & Lewis, 1977). Considerable differences were found in the duration of resistance in stored tubers (Bhatia & Young, 1985). Also the period of maximal resistance could be different. The tubers of cv. Bzura were highly resistant in October, but susceptible in December. By contrast, those of cv. Sokół were susceptible in October, but highly resistant in December (Świeżyński et al., 1993a, 1997c). Similar differences, depending on tuber evaluation time (September versus October), were found by Darsow (1983) in other potato genotypes.

An increase in resistance of wound-healed tubers was more apparent in clones with a higher level of tuber resistance (Deahl et al., 1974; Bjor, 1987).

Tuber resistance could be associated with the tendency to localise the pathogen in the invaded tissue. In tubers of cv. Pimpernel many infection sites were noted, but in most of them the growth of the pathogen was arrested in thread-like necroses (Lapwood, 1967). In cv. Pentland Crown the infections were more frequently localised in thread lesions than in cv. Majestic possessing less resistant tubers (Malcolmson, 1981). There are earlier reports that at low temperatures the fungus may be unable to survive in necrotic tuber tissues of some cultivars (Ullrich, 1970; Schöber & Höppner, 1972).

In cultivars carrying R-genes (see the section on inheritance of resistance) and showing an incompatible reaction in the foliage, tubers may also appear incompatible. However often the presence of R-genes causes only a delayed fungus invasion into tubers and sometimes there is no detectable effect. Among the first four R-genes (R1–R4), the gene R1 was found to be most frequently effective in tubers, but its expression depended to a large extent on potato genotype and testing conditions (Lapwood & McKee, 1961; Roer & Toxopeus, 1961; Davila, 1964; Ullrich, 1965; Deahl & Sinden, 1973; Yashina & Erokhina, 1976; Zacharius et al., 1976; Doke, 1982). The expression of R-gene based resistance declined with prolonged tuber storage (Serov, 1975; Chalenko et al., 1980; Allen & Friend, 1983). Tubers may require suitable pre-treatment to express the hypersensitive reaction. Furuichi et al. (1979) found that cells of tuber slices do not acquire the hypersensitive reactivity immediately, but 16–20 h after cutting and the process requires protein synthesis.

In some cultivars, e.g. Mittelfrühe and Brda, resistance to *P. infestans* is detectable in tuber skin but not, or much less, in tuber flesh (Durska, 1975). Such genotypes were also found in segregating potato progenies (Świeżyński et al., 1997a). There are cultivars in which the outer cortex layers are very resistant to colonisation by *P. infestans* (Pathak & Clarke, 1987). A barrier to *P. infestans* in the outer cortex of the tuber has been reported to be present in several potato cultivars (Toxopeus, 1961; Lapwood, 1965).

Evaluation of tuber resistance

Schöber (1987) and Dorrance & Inglis (1998) compiled data on various procedures used to evaluate tuber resistance.

It might be expected that resistance evaluation, based on natural infection in the field, would be most reliable. However it is difficult to provide a satisfactory infection pressure in the field and repeatable testing conditions (Lapwood, 1965; Ullrich, 1967; Schöber, 1987; Dorrance & Inglis, 1998; Platt & Tai, 1998). In addition, if tubers become infected from foliage, testing results are biased by foliar resistance of the evaluated genotypes (Colon & Budding, 1989). Therefore, if natural infection is evaluated in cultivar assessment it is often supplemented with various laboratory methods (Schöber, 1987). Colon & Budding (1989) suggested an evaluation under field conditions - by inoculating lifted tubers after foliage destruction - this eliminates the bias caused by foliage resistance.

For testing in the laboratory suitable inoculum must be used and tubers should be properly pre-treated. To overcome any specific resistance, an attempt is usually made to use a virulent fungus inoculum. This is not always easy to achieve. According to Schöber (1987) the applied *P. infestans* inoculum contained from three (1.2.4) to nine (1.2.3.4.7.8.9.10.11) virulence factors, depending on the country. The temperature at which the tubers are tested, inoculum concentration and mixtures of isolates versus single isolates could influence significantly the relative tuber resistance of individual potato genotypes (Darsow, 1987a). Pathogenicity of the inoculum (viability of zoospores) may last longer if tuber extract is added (Sobkowiak et al., 1997). Virus infection was sometimes found to modify the reaction of tuber slices (Barrientos, 1980; Schöber & Weidemann, 1982; Darsow & Wulfert, 1989).

It was noted that parasitic bacteria may reduce the pathogenicity of *P. infestans* (Lewosz & Hołubowska, 1999). Indications were also found that bacteria antagonistic to *P. infestans* present on inoculated tubers may reduce their infection (Clulow et al., 1995).

Weindlmayr (1961) did not notice much influence of short days on tuber resistance, but Fehrmann (1963) reports that a slight reduction in resistance may be found in such conditions. Tubers from different planting dates, harvested on the same date, did show a similar resistance level in Scotland (Malcolmson, 1981) and in Norway (Bjor, 1987), but in Poland their resistance was found to decrease with earlier planting date (Ciesiewicz, 1967).

Fehrmann (1963) reported that storage at various temperatures did not detectably influence the susceptibility of tubers if they were kept at 20 °C for 12–24 h before inoculation.

A delay between harvest and inoculation dates was sometimes found to increase considerably the resistance level. This effect depended on the cultivar tested (Malcolmson, 1981; Stewart et al., 1983; Bjor, 1987).

In many reports it is pointed out that results from laboratory tests in different years may differ considerably (Lapwood, 1967; Stewart et al., 1983; Darsow, 1987a). This may be due partly to the already reported differences between cultivars in the period of maximal resistance (Darsow, 1983; Świeżyński et al., 1993a, 1997c).

There were several attempts to compare the relative advantage of various laboratory evaluation methods (Lapwood, 1965, 1967; Durska, 1975; Pietkiewicz & Jellis, 1976; Dorrance & Inglis, 1998). The widest acceptance appears to have been found for the evaluation of whole tubers and the evaluation of tuber slices, both

modified in various ways.

According to Stewart et al. (1983), in Scotland undamaged whole tubers are spray-inoculated on the day of harvest and the percentage of blighted tubers is evaluated two weeks later. The testing results may depend on the year and on the harvest date (Darsow, 1983; Stewart et al., 1983).

Bjor (1987) found that inoculation of whole tubers on the day of harvest presented practical difficulties. Based on his results, in cultivar assessment in Norway tubers are harvested one to seven days before inoculation. In one half of the replications they are superficially wounded with nail points 2 mm long (one day prior to inoculation), as wounding was found sometimes to improve the discrimination between resistant and susceptible cultivars. This type of wounding tubers before inoculation has been also applied by Świeżyński et al. (1991).

Whole tubers, originating from first year seedlings grown in pots in a greenhouse, were used to obtain a preliminary evaluation of tuber blight resistance in breeding work. They could be undamaged (Wastie et al., 1987, 1993) or wounded (Darsow, 1992). Stewart et al. (1996) found that the procedure of Wastie et al. (1987) is also suitable for the evaluation of advanced breeders selections.

If the resistance is evaluated in tuber slices, the widest acceptance has been found for the method of Lapwood (1965) in which tuber slices are inoculated on one side and the effects are evaluated on the other side of the slice. The method is applied in various modifications.

In Braunschweig, Germany, single tuber slices 10 mm thick are kept at 15 °C after inoculation and repeatedly evaluated for several days. The slices are inoculated 24 h after cutting, as this was found to improve the evaluation conditions (Schöber & Höppner, 1972).

Darsow (1987a) reports that in Gross Lüsewitz, Germany, 11 mm thick single tuber slices are inoculated just after cutting and are kept after inoculation at 18–19 °C. The slices are repeatedly evaluated for several days. Darsow (1986) reports that wound healing prior to inoculation was not desirable. Harvest date, testing period and breaking tuber dormancy were found to influence the results of the test (Darsow, 1988). Results could also depend on tuber storage temperature prior to inoculation and on tuber size (Darsow, 1987b).

In Młochów, Poland, unseparated double slices each 10 mm thick are used. A drop of inoculum is introduced between both slices just after cutting. The inoculated slices are maintained at 16 °C and the results evaluated once, 6 days after inoculation (Świeżyński et al., 1991).

Comparison of the results of tuber resistance evaluations from various countries

If similar evaluation methods were applied, consistent results could be obtained (Schöber & Schiessendoppler, 1983). However, results from different countries may differ considerably. Świeżyński et al. (1998) compiled descriptions of 137 major potato cultivars from Europe and North America. If only data expressed or transformed into a 9-grade scale of increasing resistance are considered, for 80 cultivars descriptions

were available from more than one country. In six cultivars description differences of 3 grades were found, in seven cultivars they differed 4 grades, in five cultivars they differed 5 grades and in two cultivars the differences amounted to 6 grades. Also the mean level of tuber resistance evaluations could differ considerably. Świeżyński & Domański (1998) found that the mean resistance level of cultivars described in both The Netherlands and Germany differed by about one grade, and resistance evaluations in Poland appear to differ even more from the evaluations in these countries. It follows that evaluations in various countries are far from being consistent. Recent analysis of cultivar assessment data from five European countries demonstrated the extent of discrepancies (Świeżyński et al., 2001). The authors suggested that to reduce differences between countries the use of agreed standard cultivars and utilisation of more similar evaluation methods should be effective.

Sources of tuber resistance to *P. infestans*

Resistant cultivars. Horackova (1996) evaluated a collection of 242 potato genotypes and found among them no cultivars with a high tuber resistance level. Świeżyński et al. (1998) compiled descriptions of 137 major potato cultivars from Europe and North America and reported the highest resistance levels in cvs Hydra, Jubel and Nikita. Earlier, Świeżyński (1988) listed the 22 cultivars with the highest tuber resistance from the description of European cvs, compiled by Stegemann & Schnick (1985). Among them four cultivars, Blanik, Orion, Parel and Pimpernel, had resistant tubers according to at least two descriptions. Stewart et al. (1996) used cvs Cara and Stormont Enterprise as standards of tuber resistance. Wastie et al. (1991) report high resistance to *P. infestans* in the foliage and tubers of the cvs Torridon, Brodick and Stirling. According to German cultivar assessment data, the highest level of tuber resistance is in cv. Tristan (Anon., 1998). Siczka et al. (1999) compared resistant cultivars from various countries and found the highest tuber resistance in the Polish cv. Meduza. In Belarus the highest level of foliage and tuber resistance is found in late maturing cvs Atlant and Suzorye (Banadyseva, 1997).

Umamura (1974) reports that among evaluated progenies the highest proportion of resistant tubers was obtained from the cross Eniwa × Hokkai No. 51. Zadina (1991), who evaluated tuber resistance in 23 progenies, found a high proportion of resistant tubers in progenies of cvs Rheinhort, Saphir, Oda, Hera and Apollo.

Resistant breeders selections. There are several reports that clones outstanding in tuber resistance to *P. infestans* and interesting from the point of view of other characters were obtained in breeding work (Świeżyński et al., 1997d; Darsow, 1998; Siczka et al., 1999). Clones with tubers resistant to *P. infestans* were also obtained by somatic hybridisation (Rasmussen et al., 1998).

Resistant potato relatives in gene banks. We consider here only data with information on tuber resistance. In the germplasm collection of the International Potato Center, of 141 evaluated clones 41 had resistant tubers (Anon., 1985). Darsow & Hinze (1991)

evaluated the frequency of resistant tubers in various species. Using a criterion of resistance of at least 5.8 on a 9-grade scale of increasing resistance, they found over 80% of genotypes with resistant tubers in the following *Solanum* species: *S. bulbocastanum*, *S. cardiophyllum*, *S. demissum*, *S. ehrenbergii*, *S. morelliformae*, *S. pinnatisectum*, *S. sambucinum* and *S. trifidum*. In a more detailed evaluation of 188 accessions of *S. demissum* Darsow & Schüler (1998) found that 19% of the accessions had highly resistant tubers, receiving scores of 8 or 9. Podgaetskij (1997) demonstrated that inbreeding combined with selection may considerably increase the level of tuber resistance in resistant accessions of *S. stoloniferum* and *S. demissum*. Zarzycka (1988) compared the tuber resistance in various resistance sources utilised at the Młochów Research Center. She found the highest resistance level in two accessions of *S. demissum* (PI 160221 and GLKS 78.10/43) and in *S. stoloniferum* GLKS 69.23/63R.

Correlations of tuber resistance to *P. infestans*

Correlations between resistance of whole tubers, resistance of tuber slices and foliage resistance to P. infestans. Yashina et al. (1974) evaluated the correlation between resistance in leaflets and tubers in 10 potato progenies, finding a range of correlation coefficients from $r=+0.01$ to $r=+0.32$.

Stewart et al. (1992) found no evidence of a strong genetic correlation between foliage and tuber resistance to late blight. Later Stewart et al. (1994) evaluated in five unselected progenies the correlation between foliage resistance in field grown plants and resistance of whole tubers obtained in a glasshouse. The progenies originated from crosses between a resistant and a susceptible partner. Inoculum was believed to eliminate the resistance due to the presence of R-genes. In individual progenies the correlation coefficients ranged from $r=+0.66$ to $r=+0.88$.

Świeżyński et al. (1991, 1997a) evaluated unselected diploid and tetraploid potato progenies obtained from parents in which the resistance to *P. infestans* originated from wild ancestors. In these progenies R-genes were likely to segregate, which were not overcome by the fungus isolates used for inoculations. Depending on the progeny, the correlation coefficients between resistance in whole tubers and that in tuber slices ranged from $r=-0.29$ to $r=+0.44$. A positive correlation was more frequent. In two progenies genotypes were identified with resistant whole tubers, but susceptible tuber slices. The correlation coefficients between resistance of detached leaflets and resistance of tuber slices ranged from $r=-0.01$ to $r=+0.70$. They were usually slightly higher than those between detached leaflets and whole tubers.

There are also indirect indications that different factors may operate in the reaction of whole tubers and in the reaction of tuber flesh. Flier et al. (1998) evaluated the pathogenicity of various *P. infestans* isolates to tubers of the susceptible cv. Bintje. They found significant differences in pathogenicity among isolates, but no correlation between their ability to infect undamaged tubers and the extent of their subsequent spread in the tuber tissues.

There are several reports that potato genotypes may have resistant foliage and susceptible tubers, but much less frequent are genotypes with susceptible foliage and

resistant tubers. This was reported by Roer & Toxopeus (1961) who also cite earlier papers with similar observations, and by Chadaeva (1974). Świeżyński et al. (1997a) attempted to find genotypes with resistant detached leaflets and susceptible tuber slices in eight potato progenies, but found no genotype with this type of reaction.

Wound healing before inoculation of tuber tissues increased the correlation between the resistance in foliage and tubers. Deahl et al. (1974) evaluated 26 clones, inoculating cortical tuber tissues either not healed or healed for 48 h before inoculation. Only after healing the tubers was a positive correlation found between tuber resistance and foliage resistance in field conditions ($r=+0.87$). Doko (1982) evaluated the incompatible reaction to *P. infestans* in 12 potato cultivars carrying some of the genes R1–R4. Comparing the frequency of necrotic lesions in leaflets and the frequency of killed cells in fresh and aged tuber slices, he found a significant positive correlation after inoculation of aged tuber slices ($r=+0.639$), but for fresh slices it was minimal ($r=+0.063$).

There are many reports, e.g. Toxopeus (1958), Świeżyński (1990b) and Platt & Tai (1998), that in potato cultivars there is a positive, but rather loose correlation between foliage and tuber resistance. Durska (1975), who evaluated Polish potato cultivars, found a very weak correlation between the degree of natural infection in foliage and tubers ($r=+0.183$). She found a much closer correlation between resistance in detached leaflets and in tuber slices ($r=+0.628$) or between resistance in detached leaflets and resistance in whole tubers ($r=+0.570$). Similar results obtained Pietkiewicz (1976).

Correlation between tuber resistance and maturity or early tuber bulking. In unselected potato progenies Świeżyński et al. (1991) found correlation coefficients between length of vegetative period and resistance in tuber slices ranging in individual progenies from $r=+0.11$ to $r=+0.38$. Further evaluation has shown (Świeżyński et al., 1993b) that in these progenies no early maturing genotypes were present, which would show the highest resistance level found in these families (both in whole tubers or in tuber slices). Analysing another group of unselected progenies, Świeżyński et al. (1997a) usually obtained a weak positive correlation between tuber resistance and length of vegetative period and a weak negative correlation between tuber resistance and tuber yield at early harvest.

In the evaluation of potato cultivars, tuber resistance also tended to be negatively correlated with length of the vegetative period, but it was less close than the negative correlation between foliage resistance and length of the vegetative period (Toxopeus, 1958; Świeżyński, 1990b). In the respective correlation tables there was a deficit of late maturing cultivars with susceptible tubers. Such cultivars are probably not acceptable and could be eliminated in the breeding work.

Correlation between tuber resistance and various desirable characters. In unselected potato progenies Świeżyński et al. (1997a) generally found a very weak correlation between resistance of whole tubers or resistance of tuber slices and regularity of tuber shape. However the tuber shape in genotypes showing the highest level of

resistance in tuber slices was on average less regular when compared with the mid-parent value. Darsow & Oertel (1986) noted that seedlings resistant to *P. infestans* tend to be inferior in general tuber appearance. Styszko & Ohanowicz (1996) compared data for 103 potato cultivars and advanced breeders selections evaluated in statutory trials. They found a weak negative correlation between taste and tuber resistance to *P. infestans*.

Inheritance of tuber resistance to *P. infestans*

Most available information is based on foliage reaction to *P. infestans*. Therefore data on inheritance of potato resistance and those referring specifically to the tubers will be treated separately.

Inheritance of potato resistance to P. infestans. Eleven dominant major genes (R1–R11), providing specific resistance to *P. infestans*, have been described in resistant hybrids originating from *S. demissum*. Similar genes have been described in some other resistant species and other but not described ones are likely to exist. Such genes are often referred to as R-genes (Malcolmson & Black, 1966; Skidmore & Shattock, 1985). Individual R-genes differ in expression (Turkensteen, 1989; Stewart & Gourlay, 1995) and, as was reported in the previous section, are not necessarily expressed in the tubers. There are indications that the expression of R-genes may be modified by other genes (El-Kharbotly et al., 1996b; Ordonez et al., 1997; Trognitz, 1998). There are no reports of presence of R-genes in potato cultivars of purely *S. tuberosum* origin. The first R-genes have already been mapped on the potato genome (El-Kharbotly et al., 1994, 1996a; Li et al., 1998). A recessive gene, determining specific resistance, has been described in *S. stoloniferum* (Schick & Schick, 1961).

There were various attempts to classify minor genes for resistance. It was assumed that they provide non-specific resistance, independent of the fungus virulence. Van der Zaag (1959) suggested separating them into those responsible respectively for fungus entrance, its spread and sporulation. Progress of research in this area was summarised by Umaerus et al. (1983), Ross (1986), Wastie (1991) and Umaerus & Umaerus (1994). It does not appear to have contributed much to our understanding of the inheritance of resistance to *P. infestans*.

Leonards-Schippers et al. (1994) mapped QTL in a potato progeny segregating for late blight resistance, using two fungus isolates differing in virulence. They found loci contributing to resistance in 11 segments of 9 chromosomes. Some of them appear to show isolate specificity. Meyer et al. (1998) found a multiallelic locus in chromosome VIII, contributing significantly to the expression of resistance to *P. infestans*.

A transgression of resistance in the progeny was observed by several authors (Bonde et al., 1940; Bukasov & Kameraz, 1972; Świeżyński et al., 1997b). Darsow (1995) noted that in interspecific crosses the resistance is often below average if it comes from the male parent. In successive backcrosses with susceptible partners the resistance found in interspecific hybrids did often decrease quickly (Ross, 1986; Darsow, 1995).

Inheritance of resistance to P. infestans in potato tubers. Świeżyński et al. (1997c) evaluated the segregation for resistance in unselected potato progenies obtained from parents differing in resistance level; the resistant ones were likely to carry R-genes originating from wild *Solanum* species. This segregation indicated the presence of major genes if the resistance was evaluated in tuber slices, but not if it was evaluated in whole tubers.

Genotypes with increased resistance compared with the more resistant parent were found in several progenies both if whole tubers and if tuber slices were evaluated (Świeżyński et al., 1993b, 1997a). De,Maine (1978) found that a dihaploid of cv. Pentland Crown was more resistant in tubers to *P. infestans* than its tetraploid parent.

Tubers of potato genotypes carrying R-genes tended to be more resistant when compared with those without R-genes. This was found in the evaluation of 882 cultivars and breeders selections (Darsow et al., 1987) and in the cultivar assessment data from Germany and The Netherlands (Świeżyński, 1990b).

Breeding potato cultivars with tubers resistant to *P. infestans*

As noticed by Umaerus & Umaerus (1994), tuber testing is included in most programmes of breeding for resistance to *P. infestans*. It is reported as an element of the breeding programme in Scotland (Bradshaw et al., 1995), in France (Chatot et al., 1995) and in Poland (Sieczka et al., 1997). Probably the greatest experience in breeding for resistance to *P. infestans* with special attention to tuber resistance has been collected in the Federal Center for Breeding Research at Gross Lüsewitz, Germany. Recently Darsow (1995, 1998) described the breeding methods and achievement of this center. The objective is to develop progenitors delivered to potato breeders, superior in various characteristics; one of the most important characteristics is foliage and tuber resistance to *P. infestans*. Several resistance sources are utilised and the breeding materials are evaluated in various conditions and with different methods. The resistance originates mainly from *S. demissum* and *S. stoloniferum*, but there are also backcrossing programmes with *S. polytrichon*, *S. papita*, *S. verrucosum* and *S. bulbocastanum*.

Tuber resistance is tested several times during the breeding cycle. After preliminary evaluation of glasshouse-grown first year seedlings (Darsow, 1992), the seedlings are evaluated in the second to sixth years using tuber slice tests, according to Darsow (1987a). In the third to sixth years they are also evaluated using the method of Schöber & Höppner (1972). Whole tubers are evaluated in the fourth to sixth years of the breeding cycle according to Darsow (1983). For inoculations a mixture of three fungal pathotypes is used with respective virulence factors: 1.2.3.4.5.6.7.(8).10.11; 1.2.3.4.6.7.8.(10).11 and 1.2.3.4.5.6.7.10.11. It is attempted to combine resistance to *P. infestans* in foliage and tubers with several other desired characters. A reasonable level of resistance and quality is reported in the best progenitors delivered to breeders.

Evaluation of progress in breeding potatoes with tubers resistant to P. infestans. Świeżyński (1988) compared cultivars released respectively before 1970, in the period

1970–1979 or after 1979, basing on characteristics of European potato cultivars of Stegemann & Schnick (1985). No differences between these release periods were found in the frequency of cultivars with tubers resistant to *P. infestans*. A recent evaluation of breeding progress in the last 20 years (1976–1996) in Germany, The Netherlands and Poland has shown that in this period there was very little progress in the mean level of foliage resistance and no detectable progress in mean tuber resistance to *P. infestans* in potato cultivars of these countries (Świeżyński & Domański, 1998). Also the Federal Center for Breeding Research at Gross Lüsewitz has not had much success in this respect. If progenitors delivered by it to breeders in the period 1991–1998 are compared with those delivered in the period 1986–1989, an improvement may be noted in some important characteristics, but there is no progress in the mean level of tuber resistance to *P. infestans* (Darsow, 1998).

Discussion

Hypersensitive reaction - R-genes - durability of resistance to P. infestans. Potato tubers of susceptible cultivars, not suspected to possess R-genes, may show necrotic defence reactions (Ullrich, 1970; Lapwood, 1977). Coffey & Gees (1991) cite several reports indicating that in cytological examinations the non-specific resistance does not differ from the race-specific one in potato - *P. infestans* interactions. This means that hypersensitive reactions are not limited to genotypes carrying R-genes. Some R-genes are likely to contribute to durable resistance to *P. infestans* in the potato (Świeżyński et al., 1996). Single genes are also reported to contribute to durable resistance in other, similar pathosystems, e.g. in wheat resistance to *Puccinia graminis* or in barley resistance to *Erysiphe graminis* (Wolfe & Gessler, 1992). Johnson, who introduced the term durable resistance, has pointed out that no single genetic model is appropriate to distinguish between durable and non durable types of resistance (Johnson, 1993). Kamoun et al. (1999) comment that in plants resistant to oomycetes, hypersensitive response is the major defence reaction, and the extent to which durable nonhost or partial resistance involves genetic components that are distinct from R-genes remains unclear. All these data indicate that in attempts to breed potato cultivars with durable resistance to *P. infestans*, it is necessary to consider the risk of obtaining a specific resistance which will eventually break down. This risk must not necessarily increase if R-genes are utilised which provide a resistance not breaking down, despite attempts to overcome it.

Inheritance of tuber resistance to P. infestans. It is evident from this review that the information on the inheritance of tuber resistance to *P. infestans* is very scarce. One of the likely reasons for this scarcity is the fact that the expression of resistance genes depends to a large extent on testing conditions. Therefore it is not easy to separate genetic effects and to obtain repeatable results. The transgression observed in segregating families indicates that the resistance may depend, among others, on recessive genes or suitable gene combinations. It was found that in some testing conditions a genetic correlation between foliage and tuber resistance becomes

apparent, which indicates the presence of common genetic determinants. Several types of tuber resistance could be recognised. However the genetic background of the different types of tuber resistance is still obscure and it is not known to what extent it is possible to combine them in one genotype.

Negative correlations of tuber resistance to P. infestans. It follows from the review that some negative correlation exists between tuber resistance and early maturity; possibly also between tuber resistance and tuber quality. It could be ascribed to negative pleiotropic effects or to genetic linkage.

A negative correlation between early maturity and tuber resistance was noted in the segregation of potato families (Świeżyński et al., 1991, 1997a). Also a negative correlation between early maturity and foliage resistance is known to exist (Colon et al., 1995). It may be suspected that there are some genes contributing to resistance which negatively influence the rate of plant growth or tuber growth. Fortunately the negative correlation between early maturity and tuber resistance appears to be only weakly expressed and may not limit severely the breeding progress.

The high level of resistance to *P. infestans* originates from wild species and it is likely that resistance genes are linked to genes negatively affecting tuber quality. Such a linkage could be responsible for the quick reduction in resistance level observed in the backcross breeding programmes, as elimination of genotypes with inferior quality may at the same time eliminate those carrying genes for resistance.

How can we make progress in breeding potatoes with tubers resistant to P. infestans? The obvious objective is to combine the various types of tuber resistance which have already been identified. Based on data presented in this review it seems desirable to combine high resistance in growing tubers with high tuber flesh resistance at harvest time and possibly with the reported ability to kill the invading fungus in tubers of some genotypes kept at low temperature. More research is needed to find methods suitable for the evaluation of resistance in growing tubers and to check how useful the evaluation of tuber flesh resistance at low temperatures could be, as reported by Schöber & Höppner (1972). It is necessary to repeat evaluations, as considerable effects of years and testing dates are often found. Therefore it is important to apply, as far as is practicable, non laborious individual tests. It appears that until now, combining various types of tuber resistance has not been sufficiently attempted by potato breeders. This could be a way to get progress in breeding for tuber resistance. As potato genotypes with resistant tubers were also found to be resistant in foliage, progress in tuber resistance is likely also to increase the foliage resistance to *P. infestans*.

With new achievements in understanding the molecular aspects of the potato - *P. infestans* interaction and progress in genetic engineering techniques a breakthrough in resistance breeding may be expected (e.g. Staskawicz et al., 1995; Hammond-Kosack et al., 1998; Stahl et al., 1998; Kamoun et al., 1999). It is still difficult to predict how soon this type of approach will be able to supplement or to replace the traditional breeding work. Therefore at present it seems important to utilise effectively resistance sources originating from more traditional procedures.

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