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Durable resistance to late blight (*Phytophthora infestans*) in old potato cultivars

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Abstract

Twenty-two R gene-free cultivars, introduced between 1900 and 1954, were field-tested for their level of partial resistance to a complex race of *Phytophthora infestans*. Disease assessments, expressed as areas under the disease progress curve, appeared closely correlated to resistance ratings given between 1929 and 1954. This, and the stability in time since 1929 of the ratings in the Dutch Descriptive List of Varieties of Field Crops, suggest that the resistance concerned is durable. Lesion growth rate was found to be a very important component of resistance in these cultivars and also in more recently introduced ones, whereas latent period varied little between the cultivars. The most resistant cultivars were Robijn, Populair, Pimpernel, Libertas and Surprise, which were also among the latest maturing in the material. These five cultivars are closely related and may have the same resistance genes.

Abbreviations: ADPC = area under the disease progress curve; LGR = lesion growth rate; LP = latent period.

Introduction

Potato late blight, caused by *Phytophthora infestans* (Mont.) de Bary, is an important fungal disease of potato worldwide. Although application of agrochemicals against this disease still is common practice, financial costs and unfavourable environmental consequences render host resistance a more desirable means of protection. In developing countries, knowledge and financial input are insufficient to effectively apply fungicides. To relieve these problems, late blight resistance is an important objective of most potato breeding programmes.

Breeding for resistance to late blight has a long history. Potatoes were first introduced from South America into Europe in the sixteenth century [Glendinning, 1983]. The pathogen arrived in Europe much later, around 1840 [Large, 1940], probably introduced with potatoes from Mexico, the centre of origin of the pathogen [Fry and Spielman, 1991; Fry *et al.*, 1993]. In the early years of potato cultivation in Europe, true seed was commonly used for propagation, to produce virus-free seed potatoes. A large part of the *S. tuberosum* populations that had by 1840 evolved by the repeated use of true seed, was eliminated by late blight [Glendinning, 1983]. However, part of these populations survived the epidemic of 1845–1846, and their descendants were submitted to continuous natural selection in the presence of disease. This 'natural' selection continued through

the second half of the nineteenth century, when breeding and seed tuber production began to replace the traditional on-farm selection but seed potato growers continued to lay emphasis on late blight resistance [Glendinning, 1983].

Shortly after the first outbreaks of late blight in Europe and the United States, the Mexican species *S. demissum* Lindl., also described as *Solanum utile* Klotzsch, was already known as resistant to late blight [Lindley, 1848; Jühlke, 1849]. At that time, neither the fungal nature of the disease, nor the principles of genetics were common knowledge, and there was a widespread belief that late blight was due to degeneration of the potato, caused by continuous vegetative propagation [Lindley, 1848]. *Solanum demissum* was tried as an alternative crop plant that could replace the late blight-threatened potato, but found unsuitable due to the bad quality and low yield of the tubers. Moreover, the genotypes of the species that were available were found to be susceptible to late blight both in Great Britain [Lindley, 1848] and in Germany [Jühlke, 1849]. Although (male-sterile) *S. demissum* × *S. tuberosum* hybrids were derived by Klotzsch in 1851 and brought into trade as 'Bastard–Zuckerkartoffel' by F.A. Haage Jr., they were not as resistant to late blight as Klotzsch initially claimed [Focke, 1881]. It is therefore unlikely that these hybrids were used for further breeding, although this cannot be excluded. Therefore, there is a slight possibility that resistance genes from these early *S. demissum* introductions were transferred to *S. tuberosum*. These early hybridizations with *S. demissum* had apparently been forgotten when, in 1909, *S. demissum* was rediscovered as a source of resistance to late blight, as present in a sample of wild potatoes obtained from the US Department of Agriculture in Washington [Müller and Black, 1952]. The major genes for late blight resistance found in *S. demissum* were designated R genes. *S. stoloniferum*, also from Mexico, was found to have the same type of resistance [Schick *et al.*, 1958b]. The two species were incorporated into several breeding programmes and from 1930 onwards cultivars with R gene resistance appeared [Müller and Black, 1952], like Sandnudel in 1934 and Brennragis in 1936 [Schick *et al.*, 1958a]. With the introduction of chemicals which more effectively protected potato crops against *P. infestans*, interest in resistant cultivars decreased, and many recently introduced cultivars are very susceptible to late blight.

As a result of all these breeding activities of the past, two different forms of resistance to late blight can now be distinguished in potato cultivars. The first is a partial resistance type, known as field resistance, which is thought to be polygenic, non-race-specific and which, under long day conditions, appears to be associated with late maturity [Umaerus *et al.*, 1983]. This type of resistance may have been derived both from the earliest *S. tuberosum* introductions in Europe, and from *S. demissum* used as source of major resistance genes, but also carrying field resistance [Glendinning, 1983]. The second type of resistance, conferred by major genes from *S. demissum* and *S. stoloniferum*, is race-specific and provokes a hypersensitive response to incompatible, but not to compatible isolates of the pathogen [Toxopeus, 1956]. Some R genes cause a weak hypersensitive response which allows some lesions to develop, and these resistances may easily be confused with field resistance [Landeo and Turkensteen, 1989; Turkensteen, 1989; Turkensteen, 1993]. R genes can easily be manipulated in potato breeding programmes, but as R gene resistance was too short-lived and compatible races for most R genes are now common, their use is no longer advocated [Ross, 1986].

Phytophthora infestans is known to be a highly variable pathogen which easily adapts to factors restricting its development, such as systemic fungicides or host resistance based on R genes. Recently, the potential for variability has been further increased with the introduction of the A2 compatibility type and with it, the sexual mode of reproduction of the fungus in Western Europe and other parts of the world [Drenth *et al.*, 1993]. Therefore, durability is an important aspect of late blight resistance.

Van der Plank [1971] and Thurston [1971] assume that field resistance in potato to *P. infestans* is durable, as it is remarkably stable over the years. James and Fry [1983] found no evidence for cultivar–isolate interactions, indicative of race-specificity, and the cultivar–isolate interactions reported by Latin *et al.* [1981], though significant, are very small. All evidence suggests that field resistance in *S. tuberosum* is durable.

We may conclude that field resistance to *P. infestans* might be of great value in potato breeding, since it seems the only durable resistance to this disease so far identified. Successful exploitation of this resistance has been hampered by the fact that in many breeding stocks it is masked or mimicked by R genes. The study described in this paper was undertaken to collect and evaluate field resistant, R gene-free potato germplasm which could serve as starting material for breeding programmes aimed at durable resistance to *P. infestans*. To avoid R genes, 22 cultivars introduced before 1954 were selected and tested for resistance. The results are compared with those of two old susceptible cultivars and nine more recently introduced cultivars differing in resistance and maturity type. To estimate the durability of the resistance, the results are related to resistance ratings given at the time of introduction.

With respect to field resistance, breeding may be improved when screening is made for separate, complementary resistance components rather than for general levels of field resistance [Parlevliet, 1979]. For *P. infestans*, model studies by Van Oijen [1992] indicate that infection efficiency (IE) and lesion growth rate (LGR) are likely to be components with a major effect on the resistance level, whereas latent period (LP), sporulation capacity (SC) and sporulation period (SP) are much less effective. In field resistant genotypes of *S. andigena*, considered to be the ancestor of *S. tuberosum* [Burton, 1989], and *S. phureja*, IE, LGR, LP and SC all appeared reduced [Guzmán-N, 1964]. Nilsson [1981] confirmed that IE and LGR are reduced in resistant genotypes of *S. andigena* and *S. phureja* and found that the two components were correlated. However, the real importance of these components in field resistant potato cultivars, reviewed by Van Oijen [1991] is not clear since contradictory data have been reported. In the study described in this paper lesion growth rate and latent period of *P. infestans* of some field resistant cultivars were measured to find out whether these components of resistance could account for the observed field resistance, in which case breeding strategies could be more efficient when focused on these components.

Materials and methods

Plant material

Twenty cultivars introduced before 1954 and described as having good field resistance to late blight, or as being the progenitors of several resistant cultivars (Table 1), the old highly susceptible cultivars Eersteling (synonyms: Midlothian Early, Duke of York) and Bintje, and nine more recently introduced cultivars differing in resistance level and maturity type (Bildtstar, Cleopatra, Darwina, Elkana, Kardal, Krostar, Nicola, Ostara, Spunta), were chosen from the inventories of *S. tuberosum* germplasm by Hogen Esch and Zingstra [1957] and Joosten [1988]. The cv. Krostar has the R1 gene from *S. demissum* [Anonymous, 1929–1990]; this gene, and other R genes that might be present in these nine cultivars, are overcome by the complex race of the pathogen used in our experiments. The old cultivars have been tested in the past and found free of the 11 known R genes [Mooi, unpublished]. Their ancestors were *S. tuberosum* genotypes introduced before 1909, when the extensive use of *S. demissum* as a source of resistance in potato breeding programmes started [Müller and Black, 1952]. The old cultivars and their ancestry, maturity and late blight resistance, are listed in Table 1. Years and acreage of cultivation in the Netherlands, are given in Table 2. Since 1929, ratings for late blight resistance have been given in the Dutch Descriptive Lists of Cultivars of Field Crops [Anonymous, 1929–1990]. The earliest resistance rating for each cultivar was taken, corrected for minor fluctuations in average ratings, using those of cv. Alpha (7 in 1929–30, 8 in 1931–40, 7 in 1941–85 and 6 since 1986), the only partially resistant cultivar continuously on the list since 1929, as a reference.

Tubers of these cultivars were derived from the potato collections of the Agricultural Scientific Services of the Department of Agriculture and Fisheries for Scotland at East Craigs, Scotland, UK (cv. Pepo) and from a Dutch collection of old and current cultivars known as the C.O.A. collection, which was kept at Wageningen by the Dutch Committee for Research of Potato Cultivars (C.O.A.) until 1990. Some cultivars that are still current today, were available at CPRO-DLO. Test materials were multiplied in the field, as virus-free as possible, in a potato seed growing area.

Table 1. Ancestry, maturity and original late blight resistance ratings of 22 R gene-free cultivars

Cultivar	Year of introduction[a]	Ref.[b]	Cross	Maturity[c]	Blight[d]
Robijn	1926	2	Rode Star × Preferent	3	9
Pimpernel	1953	2	Populair × (Bravo × Alpha)	3½	9
Populair	1928	1	Robijn × Monopool	3	8
Victor	1954	2	Robijn × Industrie	3	8
Libertas	1946	2	Record × ((Bravo × Energie) × (Rode Star × Pepo))	4½	8
Irene	1953	2	Furore × (Rode Star × Pepo)	5	8
Furore	1930	2	Rode Star × Alpha	5	8
Surprise	1954	2	Noordeling × Libertas	5½	8
Noordeling	1928	2	Bravo × Jam	6	8
Bevelander	1925	2	Bravo × Preferent	6½	8
Rode Star	1909	2	Prof. Wohltmann × Erica	4	7
Alpha[e]	1925	2	Paul Kruger × Preferent	4	7
Gelderse Rode	?	2	unknown; very old Dutch cultivar	5	7 Ref. 2
Gineke	1950	2	(Rode Star × Pepo) × Record	5	7
Hindenburg[e]	1916	1	Ismene × Jubel	4	?
Voran	1932	1	Kaiserkrone × Herbstgelbe	4	6
Industrie[e]	1900	1	Zwickauer Frühkartoffel × Simson	4½	6
Record[e]	1932	2	Trenctria × Energie	6½	6
Bravo[e]	1900	1	Zeeuwse Blauwe × Wilhelm Korn	6½	6
Pepo[e]	1919	1	Deutsches Reich × Jubel	5	5 Ref. 1
Bintje[f]	1910	2	Munstersen × Fransen	6½	2
Eersteling[f]	1900	2	Early Primrose × King Kidney	9½	2

[a] Year of introduction in country of origin.
[b] Hogen Esch and Zingstra, 1957 (1); Joosten, 1988 (2).
[c] 9 = very early; 8 = early; 7 = fairly early; 6 = medium; 5 = fairly late; 4 = late; 3 = very late.
[d] Late blight resistance at introduction, or in 1929 (earliest data), in the Netherlands [Anonymous, 1929–1990]; 9 = resistant, 3 = susceptible
[e] Not field resistant, but ancestor of several field resistant cultivars.
[f] Susceptible standards.

Fungal material

P. infestans races 1.2.3.4.5.7.10.11, used in 1987, and 1.2.3.4.5.6.7.10.11, used in 1989–1993, were taken from liquid nitrogen storage at the DLO-Research Institute for Plant Protection (IPO-DLO), Wageningen. The isolates were cultured at 15 °C and 100% RH under continuous low intensity fluorescent tube (Sylvania 'cool white' 40W tubes) illumination on detached leaves of either the susceptible cvs. Bildtstar or Eersteling, or the moderately susceptible cv. Nicola. Isolates were replaced by new ones from the same stock after a few multiplication cycles.

Inoculum was prepared by rinsing leaflets with the sporulating fungus in tap water. The sporangial suspensions were placed at 10 °C for 1–2 h to induce the release of zoospores. Spore densities were recorded by ten counts of 3.2 mm^3 samples of inoculum using a haemocytometer.

Assessment of field resistance

Field resistance was measured for three successive seasons on all old cultivars and on the susceptible more recently introduced cvs. Ostara and Bildtstar. Seven additional cultivars were tested only in the third year.

Each year the trial consisted of three randomized blocks, subdivided into strips 12 drills wide. The strips were bordered by single rows of a field resistant cultivar. In the strips, rows of four plots were laid across the hills, so that each plot contained 3 × 2 plants. Rows of plots were alternated with single rows of the moderately susceptible cv. Nicola. In each block a cultivar was represented by one plot, which was treated as a single exper-

Table 2. Cultivation in the Netherlands of 22 R gene-free cultivars, and mean area under the disease progress curve (ADPC), assessed in the field from 1991 to 1993. App. = approximately

Cultivar	Total period		Main period[a]		Best year			ADPC
	First year	Last year	Sum of acreage (1000 ha)	Number of years	Year	Acreage (1000 ha)	% of Dutch acreage	
Robijn	1927	1946	5.8	5	1942	2.1	1	0.23
Pimpernel	1955	1986	19.2	19	1968	1.5	1	0.30
Populair	1935	1955	6.0	4	1942	2.1	1	0.28
Victor	Unknown							0.42
Libertas	1946	1980	146.2	28	1959	3.1	9	0.30
Irene	1953	Present	71.1	29	1988	5.6	3	0.34
Furore	1930	1980	96.9	36	1952	5.6	3	0.41
Surprise	1954	Present	43.0	30	1968	3.0	2	0.31
Noordeling	1928	App. 1978	230.3	40	1948	15.5	7	0.42
Bevelander	1925	App. 1976	280.5	39	1943	21.2	10	0.34
Rode Star	App. 1909	App. 1965	327.7	29	1932	31.7	22	0.38
Alpha	1925	Present	121.7	55	1949	5.5	3	0.42
Geld. Rode	Unknown							0.40
Gineke	1950	App. 1976	33.9	17	1960	4.4	3	0.39
Hindenburg	Unknown							0.43
Voran	1938	1973	821.6	34	1954	56.4	33	0.39
Industrie	App. 1900	1959	230.4	24	1931	24.6	13	0.37
Record	1936	1984	177.8	32	1947	16.2	8	0.41
Bravo	App. 1900	1936			<1931			0.46
Pepo	Unknown							0.43
Bintje	App. 1910	Present	2207.1	59	1988	68.9	40	0.61
Eersteling	App. 1900	Present	276.9	59	1932	12.3	7	0.66
LSD ($P < 0.05$)								0.06

[a] Years during which the cultivar was grown on more than 0.25% of the Dutch potato acreage, in the period of 1931–1988 [Anonymous, 1949–1990].

imental unit, as described in Colon and Budding [1988].

Seed tubers were planted in a trial field with sandy soil near Wageningen, at a distance of 0.35 m in hills which were 0.75 m apart. Planting dates were April 24th in 1991, April 28th in 1992 and April 22nd in 1993. Patoran (metobromuron) was applied as a pre-emergence herbicide, and Imidan (fosmet) against Colorado potato beetles. No other pesticides were applied.

Inoculations were made when the foliage was touching between rows, in 1991 on July 15th, in 1992 on June 30th and in 1993 on June 22nd. Inoculum densities were 1.7×10^4 sporangia and 1.0×10^4 zoospores per ml in 1991, 1.1×10^4 sporangia and 2.1×10^4 zoospores per ml in 1992, and 2.4×10^4 sporangia and 0.5×10^4 zoospores per ml in 1993. Plots were thoroughly wetted by overhead sprinkling prior to inoculation, and inoculated late in the evening using a tractor-driven sprayer with a spraying arm with six nozzles placed 0.75 m apart. Pressure was kept at 2.5 bar with a propane tank. The equipment was moved across the plots at a fixed speed of about 5 km h^{-1}. The border rows of the strips were not inoculated.

After inoculation, the trial field was irrigated with overhead sprinklers every morning and evening to improve the conditions for sporulation and infection by increased humidity.

Disease assessments were made at weekly intervals. The percentage of leaf area affected by late blight was estimated for each plot using the second scale given in Colon and Budding [1988]. From these readings the area under the disease progress curve (ADPC) was calculated according to the method of Shaner and Finney (1977] and normalized as described by Fry [1978].

Field assessment of resistance components

Lesion growth rate (LGR) and latent period (LP) were assessed for the resistant old cvs. Libertas, Pimpernel and Surprise, the susceptible old cvs. Bintje and Eersteling and the nine current cultivars. Three experiments were carried out, on a trial field with sandy soil near Wageningen, in 1987, 1989 and 1990. The 1987 experiment was a detailed study of the development of late blight lesions, for which a subset of three cultivars was used. In 1989 and 1990, lesion growth rate and in 1989 latent period for all 14 cultivars was assessed.

Tubers were planted at a distance of 0.35 m in hills which were 0.75 m apart. Trials were bordered by single rows of the field resistant cultivar Pimpernel.

In 1987, the trial consisted of ten randomized blocks with one plant of each of the cvs. Bintje, Pimpernel and Libertas in each block, planted on May 22nd. On August 10th, three to eight leaflets of each plant, positioned about one third from the top of the plant, were inoculated on the lower epidermis with a 10 µl drop of inoculum with a density of 2.6×10^4 sporangia ml^{-1}. Infection percentages were around 90%. On day 4, 5, 6, 7, 8 and 11 post inoculation (p.i.), the resulting lesions were measured using a transparent mm grid, counting all mm squares covering the necrotic area. From this area an average linear lesion growth rate was obtained by converting the area into a radius as if the mostly ellipsoid lesion were circular, followed by linear regression of the resulting radius on time.

In 1989, two blocks with five plants of each genotype were planted on May 16th, and spray-inoculated on July 10th with a suspension of 4.4×10^4 sporangia ml^{-1}. Four days later, four lesions of each plant were labelled. On day 4, 6, 7 and 8 p.i., the greatest length of the lesions, usually parallel with the secondary leaf veins, and the largest width along an axis perpendicular to the first measurement, were measured. To convert these pairs of measurements into single values, the area of a corresponding ellipse was calculated as $\frac{1}{4}\pi \times \text{length} \times \text{width}$. LGR was estimated from this area for lesions that reached a final size of more than 5 mm^2, by converting the area into a radius as if the lesion were circular, followed by linear regression of the resulting radius on time. Two lesions on each of seven plants per genotype were used to assess latent period. As soon as lesions became visible, which was 4 days p.i., a strip of transparent adhesive tape was gently pressed against the lesion on the lower side of the leaf each morning. The strip was placed on a microscope slide, a drop of lactophenol-acid fuchsin was added and examined for the presence of sporangia under a microscope at 320× magnification. Lesions were sampled in this way till 7 days p.i., or until they showed sporulation. Latent periods were estimated through logistic regression as time in days after inoculation at which 50% of the finally achieved number of actually sporulating lesions was reached.

In 1990, three blocks with one plant of each genotype were planted on May 1st, and spray-inoculated on July 10th with a suspension of 3.8×10^4 sporangia ml^{-1} and 0.9×10^4 zoospores ml^{-1}. Five lesions of each plant were measured on day 5 and 7 p.i., and LGR was estimated as in the 1989 experiment.

Statistical analyses

Analyses were performed on all ADPC values, and on the LGR values larger than 0.1 mm day^{-1}. Small lesions and low LGR values were usually associated with highly necrotic lesions which did not extend beyond the originally inoculated area, whereas other lesions on the same genotype grew to a much larger size. These non-growing lesions were regarded as unsuccessful infections.

Average ADPC and LGR values and standard errors were estimated with the residual maximum likelihood (REML) method [Patterson and Thompson, 1971], using years, replicates and plots/plants as random factors and genotypes as fixed factor. Residuals were checked for uniformity.

Calculations were done with Genstat [Payne *et al.*, 1987]. All significance levels were computed at $P = 0.05$, unless stated otherwise.

Results

Epidemics resulting from the field inoculations were moderately severe; the foliage of the most susceptible genotypes was completely killed in about five weeks. In 1993, temperatures were rather low in the weeks following inoculation, and

this resulted in lower ADPC values compared with 1991 and 1992 for all genotypes. Average ADPC values of 22 old cultivars, estimated in the three years (Table 2) varied from 0.23 (most resistant) to 0.66 (most susceptible). Three years of testing allowed for a reliable separation of susceptible and resistant cultivars. Coefficients of linear correlation (r) between two years were 0.85, 0.90 and 0.95. The most resistant cultivars were Robijn and Populair. Most of those cultivars which were included because they were ancestors of resistant cultivars, had only intermediate resistance (Tables 1 and 2). ADPC values were closely correlated to resistance ratings given at introduction of the cultivars (linear correlation, $r = -0.91$, $n = 21$). ADPC values were also significantly correlated with maturity ratings, in the sense that the more resistant genotypes strongly tended to be late maturing, whereas susceptible genotypes appeared in every maturity class. This association was found with both old (Tables 1 and 2) and more recently introduced cultivars (Table 3). The ranking correlation between ADPC and maturity in Table 1 was $r = 0.85$ ($n = 15$).

Radial lesion growth in the 1987 experiment appeared to be linear (Fig. 1). Therefore, this component of resistance was assessed as linear lesion growth rate (LGR) in the other experiments. LGR of 14 cultivars, assessed in 1989 and 1990 (Table 3) significantly varied between cultivars, but there was little variation in latent period (LP, Table 3). LGR ranged from 1.14 mm day^{-1} (cv. Libertas) to 2.42 mm day^{-1} (cv. Eersteling). The coefficient of linear correlation between average LGR values from the two experiments was $r = 0.70$ ($n = 12$). LP varied less, from 4.3 to 5.8 days p.i., the average being 4.9 days p.i. LGR averaged across 1989 and 1990 was closely correlated to ADPC as measured in 1993 ($r = 0.90$, $n = 15$), while LP was less closely correlated with ADPC ($r = -0.42$, $n = 13$).

Discussion

Some of the old cultivars tested had higher levels of partial resistance to late blight than well known field resistant cultivars grown at present. Robijn and Populair in particular were highly resistant. Fry [1978] found a dosage of about 0.65 kg mancozeb ha^{-1} wk^{-1} to be sufficient to reduce ADPC to 0.02 in the partially resistant cv. Sebago (ADPC unsprayed 0.28), whereas about 1.75 kg mancozeb ha^{-1} wk^{-1} was needed to reduce disease to the same level in the susceptible cv. Hudson (ADPC unsprayed 0.50). Therefore, the resistance

Table 3. Area under the disease progress curve (ADPC; 1993), latent period (LP; 1989) in days after inoculation, and linear lesion growth rate (LGR; average of 1989 and 1990) in mm day^{-1}, of *Phytophthora infestans* race 1.2.3.4.5.6.7.10.11 on 15 potato cultivars, based on assessment in the field. n = number of lesions per genotype

Cultivar	ADPC	LP	(n)	LGR	(n)	Maturity[a]
Surprise	0.22	5.1	(13)	1.15	(44)	$5\frac{1}{2}$
Libertas	0.24	–	–	1.14	(7)	$4\frac{1}{2}$
Pimpernel	0.25	5.0	(13)	1.37	(46)	$3\frac{1}{2}$
Kardal	0.27	5.8	(13)	1.32	(47)	3
Alpha	0.33	4.3	(14)	1.65	(39)	4
Elkana	0.37	5.6	(12)	1.79	(45)	$4\frac{1}{2}$
Darwina	0.38	4.7	(14)	1.85	(45)	$4\frac{1}{2}$
Nicola	0.41	5.0	(14)	1.52	(40)	6
Spunta	0.48	5.2	(12)	1.63	(43)	7
Bildtstar	0.49	–	–	1.96	(12)	6
Krostar	0.51	4.6	(13)	2.05	(36)	7
Ostara	0.53	4.5	(12)	1.78	(30)	8
Bintje	0.54	4.6	(11)	2.41	(38)	$6\frac{1}{2}$
Cleopatra	0.60	4.5	(10)	2.26	(32)	8
Eersteling	0.60	5.1	(10)	2.42	(29)	$9\frac{1}{2}$
LSD ($P < 0.05$)	0.06	–	–	0.46	(38)	

[a] See Table 1 for explanation.

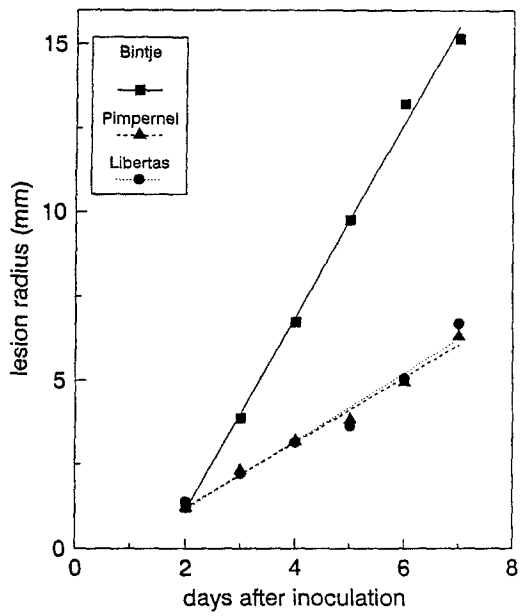

Fig. 1. Development of late blight lesions in the field in 1987 on leaves of the susceptible cultivar Bintje (n = 33) and the field resistant cultivars Libertas (n = 58) and Pimpernel (n = 63), inoculated with single 10 µl drops of inoculum containing 2.6×10^4 sporangia ml^{-1} of *P. infestans* race 1.2.3.4.5.7.10.11.

of cultivars such as Robijn (ADPC in our experiments 0.23) might be sufficient to reduce the amount of fungicide by more than 70%, compared to the amount needed on a susceptible cultivar of the same maturity.

The most resistant among the old cultivars are all rather late maturing, which is probably not a chance effect since field resistance to *P. infestans* in *S. tuberosum* is known to be associated with lateness [Toxopeus, 1958; Umaerus *et al.*, 1983]. At present, it is not known whether genetic linkage is the basis of this unfavourable association, or whether physiological factors in ageing potato plants, which occur earlier in early maturing genotypes, influence the expression of resistance genes [Toxopeus, 1958; Colon *et al.*, in preparation].

The resistance of Robijn and Populair is high, but perhaps even higher resistance levels may be obtained through accumulation of the resistance genes in these genotypes. Transgression in *S. tuberosum* of partial resistance to late blight has been reported before [Toxopeus, 1958]. All the cultivars we have tested are derived from crosses between a resistant and a susceptible or at best moderately resistant progenitor. Therefore, intercrossing the most resistant ones might result in even better resistance, although it might also result in a further deterioration of earliness.

The most resistant cultivars in the experiments, Robijn, Populair, Libertas, Pimpernel and Surprise, are all closely related. Robijn is a progenitor of Populair and Pimpernel. Libertas and Robijn are both descendants of Rode Star (= Prof. Wohltmann × Erica), and Surprise is a direct descendant of Libertas. Robijn was derived from the cross Rode Star × Preferent (= Eigenheimer × Cimbals Neue Imperator), in which both Cimbals Neue Imperator (= Imperator × Wilhelm Korn), known to be fairly resistant, and Rode Star may have contributed to the resistance. Preferent itself is only moderately resistant [Hogen Esch and Zingstra, 1957]. Imperator has been derived, through Early Rose, from Rough Purple Chili, introduced from Chile in 1851 [Glendinning, 1983]. The eight most resistant cultivars all had both Prof. Wohltmann (= Daber × Erste von Frömsdorf) and Wilhelm Korn as progenitors. Daber was introduced in 1830 from South America [Ross, 1958, cited by Glendinning, 1983], probably from Chile [Hawkes, 1956, cited by Glendinning, 1983]. In Libertas the cv. Energie (Commandant × Zomerroden), being both grandparent and great grandparent of Libertas, and also known to be fairly resistant, may have contributed to its resistance as well. Unfortunately, neither Prof. Wohltmann, nor Wilhelm Korn, Cimbals Neue Imperator or Energie were available for our experiments. The pedigrees of most of these ancestors are not known, but it is possible that they trace back to just a few genotypes. Consequently, it cannot be excluded that they share the same pool of resistance genes. Recent success in mapping quantitative trait loci (QTLs) for field resistance to late blight in *S. tuberosum* [Leonards–Schippers *et al.*, 1994] may allow for a future more precise identification of alleles involved in the resistance of these old cultivars.

Results presented here suggest that the partial resistance present in these old *S. tuberosum* cultivars is durable, since the general level of resistance now seems to be about the same as it was at the time of introduction of the cultivars, indicating that no important differential erosion of this resistance has taken place. Although we cannot

compare the two measures of resistance, as they have not been determined by the same method, it is apparent that cultivars that were much more resistant than the susceptible Bintje and Eersteling at introduction, nowadays still are relatively resistant. We have used one common, virulent isolate in our experiments. Ideally, several different isolates of the pathogen should be used, to check whether cultivar–isolate interactions are present which indicate adaptation of the pathogen population to these resistant cultivars. Such a significant, but small adaptation has been reported for tuber resistance of cv. Pimpernel in Norway [Bjor and Muledid, 1991]. However, the resistance ratings given to these cultivars during the years they were cultivated, which were derived from tests with other isolates and natural infections, show no conspicuous interactions with years, nor an increase in susceptibility during a cultivar's life span, as was also found by Van der Plank [1971]. The cultivars Alpha, Gineke and Voran were found to be partially resistant in the late blight areas of Mexico, where the widely variable population of the pathogen has every opportunity to break non-durable resistances [Niederhauser and Mills, 1953]. Some of the resistant cultivars tested in our experiments, like Bevelander and Rode Star, were cultivated on a considerable acreage for several decennia and if adaptation of the pathogen population were possible, it would most likely have taken place. However, this appears not to have happened. The cultivars Alpha, Irene and Surprise, still cultivated in the Netherlands, have been exposed to the sexual population of *P. infestans* present in Europe since around 1980 [Drenth, 1994] without apparent loss of resistance. Therefore, in accordance with Van der Plank [1971] and James and Fry [1983], it may be assumed that this resistance is durable.

Lesion growth rate appeared to be an important component of this resistance, whereas latent period hardly varied and was not closely related to field performance. The relationship of LGR with field resistance has been reported before [a.o. Weihing and O'Keefe, 1962 and Umaerus and Lihnell, 1976], but in those experiments LGR was measured only under controlled conditions in the glasshouse. The data presented in Table 3 show that also in the field LGR is an important component of late blight resistance, as was predicted by Van Oijen's [1992] model. This was found in both old and more recently introduced cultivars, some of the latter having *S. demissum* among their ancestors, which may have donated (part of) the field resistance. The correlation of the average LGR of 1989 and 1990 with the average ADPC of 1993 was so strong, that LGR may be used as a reliable indicator of field resistance in *S. tuberosum*. The low, though significant correlation between the LGR averages of 1989 and 1990 is not in agreement with this, nor with the high correlations which we have generally found between years for ADPC. Possibly this may be explained by the fact that most of the lesions (30 on each cultivar) were measured in the 1989 experiment, whereas the 1990 ten-lesions averages are less reliable. The high correlation between ADPC and LGR may be advantageous for breeding, as it can be applied in an early phase of selection when only few plants are available. Cultivars with the lowest LGR in our experiments were Libertas, Surprise, Kardal and Pimpernel. We did not assess the LGR of Robijn or Populair, but Lapwood [1961], under controlled conditions, found the lesion growth rate of Robijn to be reduced compared to that of Pimpernel.

Our results suggest that these old field resistant cultivars are valuable sources of durable resistance to late blight, although it is not clear whether this resistance can be combined with earliness. More research is urgently needed to clarify the reasons for the unfavourable association between lateness and resistance. At the moment, it is uncertain whether it is caused by genetical linkage or by physiological interactions. Nevertheless, there will always be a place for late maturing cultivars with resistance to potato late blight. In addition, in short day potato growing regions where late genotypes become much earlier maturing, these old cultivars may be very useful for resistance breeding. It may be possible to improve the resistance through accumulation and recombination of resistance genes, in which measurements of lesion growth rates may be a valuable tool, especially in the early stages of selection. It would be useful to investigate whether and to what extent this resistance could be combined with partial resistance from other sources, such as *S. demissum* and other *Solanum* species.

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