Breeding for host resistance: the key to sustainable potato production

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SUMMARY

Phytophthora infestans (Mont.) de Bary, the causal agent of late-blight disease of potato, continues to be a major limiting factor to potato production worldwide. Field trials in 2009, inoculated with two highly aggressive and commonly occurring blight strains, Blue 13 and Pink 6, demonstrated that Sárpo Mira and Axona possess high levels of resistance to these strains. Resistance in many previously resistant cultivars was severely eroded when challenged with these new genotypes. A comparison of results from eighteen trial sites across Europe over the past six years shows that Sárpo Mira has maintained high levels of resistance to all blight populations. Durable resistance such as this should enable world potato production to become more sustainable.

KEYWORDS

Phytophthora infestans, late blight, host resistance, durable resistance.

INTRODUCTION

THE NEED FOR HOST RESISTANCE

Although late-blight disease can be effectively controlled in most situations it is becoming increasingly apparent that sole reliance upon fungicide application is not appropriate. The extremely wet summers in 2007/08 in Western Europe prevented routine applications to many crops on waterlogged soils. Even in "normal" years, control is proving more difficult as new pathogen populations are often highly resistant to the once widely used phenylamide group of fungicides. Increased public concern over residues in food and the large carbon footprint of intensive agriculture have led to increased pressure to reduce inputs at all stages of the food supply chain. Organic growers are still reliant upon preparations of copper for blight control but the use of copper in such systems is an anomaly and is being questioned more and more. Finally, many commonly used fungicides, including mancozeb, widely used in mixtures to prevent emergence of resistance, are scheduled for withdrawal under recent EU directives.

While it is clear from the above that host resistance is highly desirable in the developed world, it is in the developing world where the deployment of cultivars (cvs) with confirmed, broad-spectrum resistance would hugely increase crop yield. In many countries, growers risk crop failures when

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chemical applications and advice are not affordable or unavailable. Late blight has devastating effects on yield in these circumstances (see Fig 1) and the use of host resistant cvs would go some way to alleviating this.

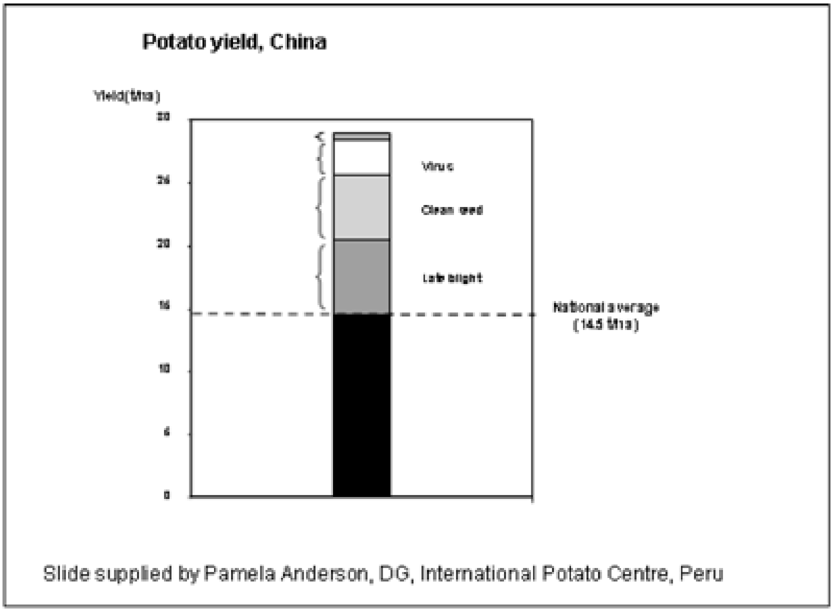

Figure 1: *potato yield in China showing the estimated effect of late blight on yield (courtesy CIP)*

SOURCES OF RESISTANCE

The first efforts to develop blight resistant cvs followed the devastating epidemics that led to the Irish Potato Famine in 1845 - 50 (Large, 1940; Salaman, 1949). These initial efforts resulted in cvs with partially successful field resistance, also known as quantitative or partial resistance (Wastie, 1991). The discovery of the major (R) genes in *Solanum demissum*, a wild species originating from Mexico, was seen by many as the "cure" for potato late blight (Reddick, 1934; Black, 1970) and became the focus of most breeding programmes during the first half of the 20th century. However, it was not long before strains emerged within pathogen populations that were able to overcome these R-genes (Malcolmson, 1969). Even the "pyramiding" of several R-genes into the same potato cv proved non-durable. The cv Pentland Dell, containing R1, R2 and R3, was initially immune to the U.K. population of *P. infestans*. Only four years after the start of commercial production, as the area planted increased, strains compatible with all three R-genes became common in the UK and control failed (Malcolmson, 1969).

As a result of the failure of available R-genes to provide durable resistance to late blight, breeders started to select for quantitative field resistance, either by selecting with races compatible with the R-genes in their material or by creating entirely R-gene free germplasm (Toxopeus, 1964). Black defined field resistance as the degree of resistance exhibited by a plant to all races of *P. infestans* to which it is not hypersensitive (Black, 1970). Black demonstrated that field resistance could be built up rapidly through hybridizations using appropriate breeding material (Black, 1970). Seedling selections had complex pedigrees tracing back to *S. demissum* but also included breeding material derived from *S. phureja* and *S. microdontum*.

Subsequent breeding programmes have utilized a wide range of wild *Solanum* spp., both as sources of major R-genes and also as part of field-resistance breeding strategies (Hawkes, 1990). Most recently, Rb genes from *S. bulbocastanum* have been used in both classical and transgenic breeding programmes and gene *Rpi-vnt1.1* from *S. venturii* has been identified and cloned (Foster *et al.*, 2009) with transformed plants of cv. Desiree containing this gene being field trialled in the UK for the first time this year. Whether or not these novel resistant lines prove durable remains to be seen.

A recent breakdown of resistance in many previously resistant cultivars has occurred in the last few years as new strains of the pathogen have become common in U.K. (Lees *et al.*, 2008). This paper aims to compare the resistance of two Sárpo cvs with that of several other resistant cvs to new strains of blight (Blue 13 and Pink 6) in field trials in 2009 and to examine the resistance of Sárpo Mira in other trials in Europe over the last few years.

MATERIALS AND METHODS

To assess the foliar resistance in a number of commercially available blight resistant cultivars as well as in Sárpo Mira and Axona, inoculated field trials were used.

Field trials in 2009 were carried out at two sites, Llanbedrgoch and Henfaes, both in North Wales. Both trials were planted in randomised 25-tuber plots and were triplicated at Llanbedrgoch and duplicated at Henfaes. Each trial contained Sárpo Mira and Axona as well as eight commercially available cvs, all purporting to have high resistance to late blight (NIAB blight rating >5 on a 1-9 score of resistance (NIAB potato variety guide, 2007). Susceptible and resistant Eucablight standard cvs, Bintje and Robijn respectively were included.

The Llanbedrgoch trial was inoculated with an isolate of strain Blue 13 (SSR genotype 13_A2) and the trial at Henfaes with an isolate of strain Pink 6 (SSR genotype 6_A1), these two genotypes representing the predominant strains within the UK population (Cooke *et al.*, 2008). The central plant of each plot (plant 3 in row 3) was sprayed with 4 x 10^4 sporangia in suspension on 13th July. Inoculated plants were bagged in plastic overnight to maintain leaf wetness and promote rapid infection. No spreader rows were used in these trials.

Scoring of the percentage of foliar late-blight in both trials was according to Cox & Large (1960). Observations were made at 3-5 day intervals. Relative Area Under Disease Progression Curve (rAUDPC) values for all cvs in each trial were calculated (Fry, 1978).

Both trials were managed under conventional agronomic practices and had received similar rates of NPK fertilizer prior to planting. Weeds were controlled with a pre-emergence application of Defy (prosulfocarb) at 5 l/ha.

RESULTS

2009 FIELD TRIALS

Llanbedrgoch, North Wales inoculated with strain Blue 13.

Highly blight-conducive conditions allowed rapid establishment and progression of the disease through plots of susceptible cultivars (cvs). Bintje, the Eucablight susceptible standard variety, had reached 90% foliar infection thirteen days post inoculation. Non-Sárpo cvs showed low levels of resistance whereas Sárpo Mira and Axona showed a slow-blighting phenotype with Robijn showing intermediate resistance (Fig. 2).

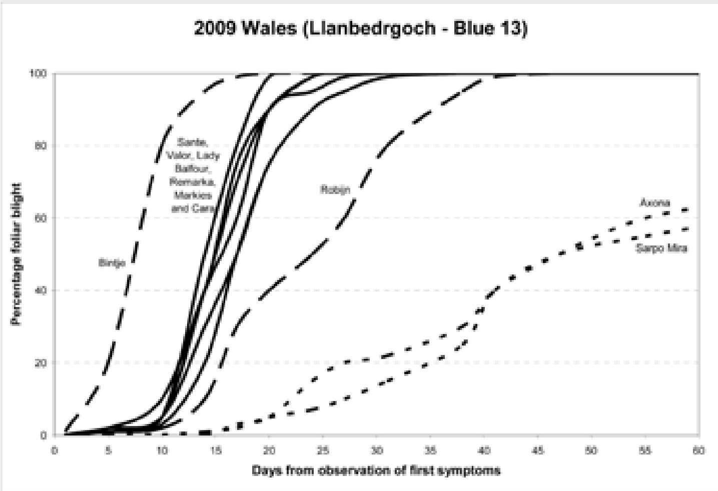

Figure 2. *Progression of foliar blight at Llanbedrgoch, North Wales in 2009 inoculated with strain Blue 13. Disease progression curves are shown for Eucablight standard cvs, Bintje (susceptible) and Robijn (resistant) and six commercially available blight-resistant cvs, all with an official NIAB foliar blight rating of five or above (source: NIAB potato variety guide 2007) and the Sárpo cvs Axona and Sárpo Mira.*

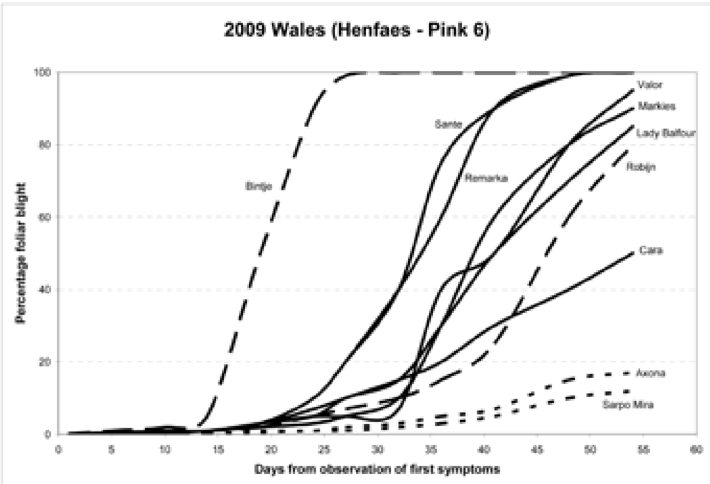

Fig. 3. *Progression of foliar blight at Henfaes Research Centre, North Wales in 2009 inoculated with strain Pink 6. Disease progression curves are shown for Eucablight standard cvs, Bintje (susceptible) and Robijn (resistant) and six commercially available blight-resistant cvs all with an official NIAB foliar blight rating of five or above (source: NIAB potato variety guide 2007) and the Sárpo cvs Axona and Sárpo Mira. Henfaes Research Centre, North Wales, inoculated with strain Pink 6.*

Similarly, conducive weather conditions enabled rapid establishment of blight. However, the subsequent progression was much slower than in the Llanbedrgoch trial (Fig. 3). Bintje reached 90% foliar infection twenty five days post inoculation, almost twice as long as it took when inoculated with strain Blue 13. Non-Sárpo cvs showed a range of rates of slow blighting and Sárpo Mira and Axona clearly showed higher levels of foliar resistance.

DURABILITY OF RESISTANCE OF SÁRPO MIRA

Sárpo Mira has been included in our field trials in Wales and Cornwall since 2004. Foliar resistance scores for this cv are shown in Table 1, calculated via the Eucablight website (www.eucablight.org) or from unpublished data of the Sárvári Research Trust.

Table 1. *rAUDPC values and 1-9 scores (where available) for Sárpo Mira, 2004-09.*

Year	Location	SSR Genotype (where known)	rAUDPC	1-9 score
2004	Wales (Llanbedrgoch)	Unknown A1	0.00	
2006	Wales (Llanbedrgoch)	Unknown	0.00	
2007	Cornwall (Duchy College)	13_A2	0.00	9.0
2007	Wales (Henfaes Research Centre))	13_A2	0.06	9.1
2007	Wales (Llanbedrgoch)	13_A2	0.06	
2008	Wales (Llanbedrgoch)	13_A2	0.25	8.1
2009	Wales (Henfaes Research Centre)	6_A1	0.02	8.6
2009	Wales (Llanbedrgoch)	13_A2	0.31	9.1

It is clear that even when challenged by isolates of strain Blue 13, Sárpo Mira expressed high or very high resistance.

Sárpo Mira has also been included in trials in many other countries in Europe over this period and has therefore been exposed to a wide range of strains *of P. infestans*. Scores for foliage blight calculated via www.eucablight.com (Fig. 5) are consistently high and rarely drop below 8.

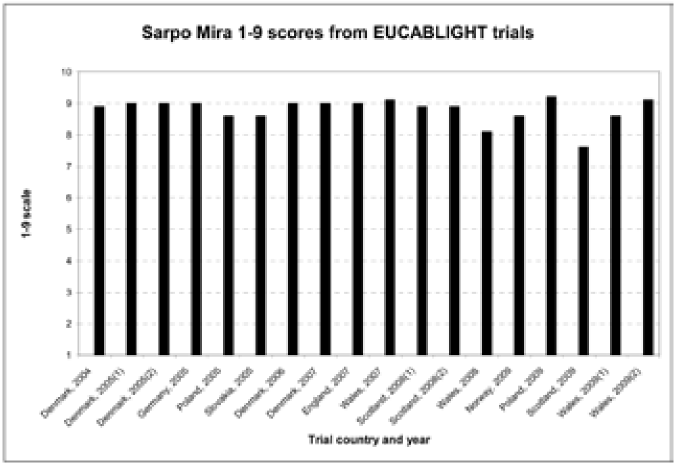

Fig. 5 *Eucablight 1-9 scores for Sárpo Mira from trial sites across Europe, 2004-09. Denmark (1) represents the Vejle site; (2) Vestsjaelland site, Scotland (1) and (2) are both sites in South Ayrshire and Wales (1) and (2) correspond to Llanbedrgoch and Henfaes respectively.*

Resistance scores, as represented by rAUDPC, for Sárpo Mira, Lady Balfour and Bintje from 2004 until 2009 (Fig. 6) show the increase in susceptibility in Lady Balfour from 2007 to close to that of Bintje where strain Blue 13 was introduced to the trials or was suspected to be present. Comparative scores for Sárpo Mira also increased but remained usefully resistant. It should be pointed out that susceptibility of Lady Balfour was high in the trial in 2004 even before strain Blue 13 was detected in North Wales.

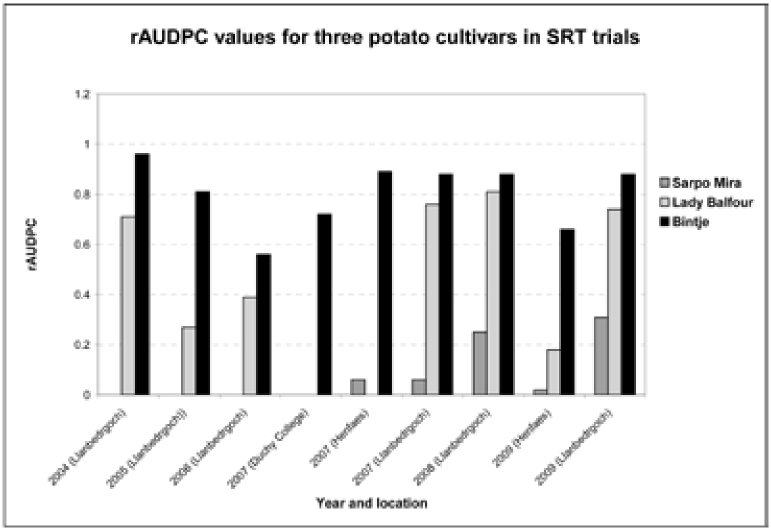

Fig. 6. *rAUDPC values for cvs Sárpo Mira, Lady Balfour and the susceptible standard, Bintje from trials over several years. Lady Balfour was not included in trials at Duchy College, Cornwall or at Henfaes in 2007. Sárpo Mira was not included at Llanbedrgoch in 2005. Sárpo Mira had an rAUDPC value of 0 in the trials at Llanbedrgoch in 2004 and 2006 and in the trial at Duchy College, Cornwall in 2007.*

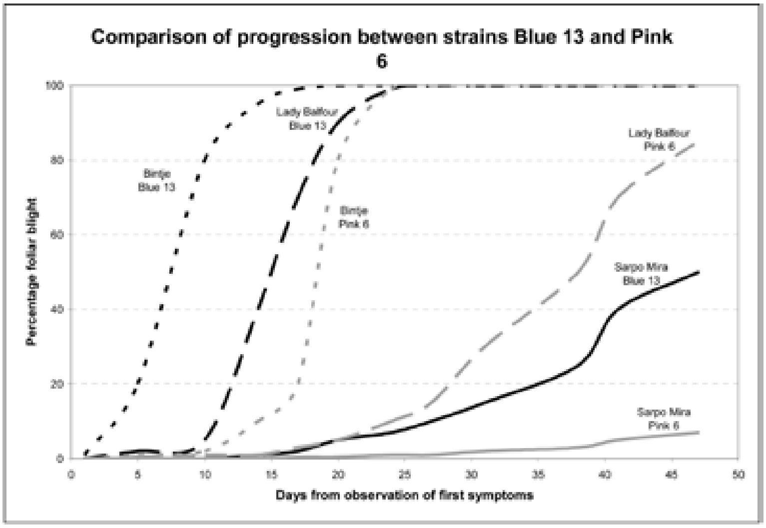

Fig.4. *Disease progress curves for three cultivars inoculated with the Blue 13 and Pink 6 strains from the trials in 2009.*

DISCUSSION

The slower disease progressions with one isolate of strain Pink 6 compared with that of one of strain Blue 13 may have been partly due to environmental factors. The trial site with strain Pink 6 had a lower rainfall and was more exposed to prevailing winds which undoubtedly reduced leaf wetness relative to that at the Blue 13 site. Also, there is a possibility that the isolate of strain Pink 6 used to inoculate the trial had a lower aggressiveness than other isolates of Pink 6 or that it had lost some of its pathogenicity due to a period in pure culture.

In the Henfaes trial inoculated with Pink 6, the resistant cvs showed various degrees of slow blighting compared to the Bintje control. Sárpo Mira and Axona were clearly the most slow blighting cvs (Fig 3). In contrast, with strain Blue 13, Sante, Valor, Lady Balfour, Markies and Cara showed some resistance until day 10 after first symptoms appeared, then progressed as rapidly as Bintje. Axona and Sárpo Mira still showed a distinct slow-blighting phenotype, albeit not as slow as with Pink 6 and Eucablight resistant control retains an intermediate slow-blighting phenotype (Fig. 2).

In conclusion, our trials show that the partial resistance of several popular cvs is eroded by strain Blue 13 which is now common and widespread in U.K. and NW Europe.
While Sárpo Mira and Axona were more susceptible to Blue 13, they have continued to retain a useful slow-blighting phenotype under extremely high blight pressure. The resistance of Sárpo Mira may be mainly due to a gene or genes within an R-gene cluster on chromosome 11 (Jadwiga Śliwka and Iga Tomczynska, personal communication). So far, this resistance has proved durable to new strains of *P. infestans*, including strain Blue 13. But if Sárpo Mira and Axona come to be grown on a large scale, there is a danger that compatible virulence genotypes may become selected in the pathogen population.

Now that new populations of *P infestans* with increased ability to overcome certain resistance genes have become common in NW Europe, the published official 1 – 9 scores used by growers to select varieties need to be updated. Table 2 compares the foliar blight scores published in Great Britain by National Institute of Agricultural Botany (NIAB) for a range of resistant cvs and the values calculated via Eucablight for our trials in 2008 and 2009

Table 2. *1-9 scores for a range of commercially available blight resistant cultivars (9=resistant, 1=susceptible). Values from field trials were calculated by Eucablight from Sárvári Research Trust field trial data.*

Cultivar	NIAB score	2008 (Blue 13)	2009 (Blue 13)	2009 (Pink 6)
Sárpo Mira	9	8.1	9.1	8.6
Axona	7	6.3	8.7	8.4
Lady Balfour	8	3.4	4.7	6.3
Markies	7	4.3	5.2	6.3
Orla	8	3.7	4.4	3.8
Sante	7	3.1	4.3	3.8
Cara	6	3.5	5.3	7.0
Valor	5	3.5	4.8	4.9

CONCLUSIONS

Sárpo Mira and Axona continue to show high resistance to all blight populations they have been exposed to, both in the UK and Europe over the past ten years as new aggressive strains have evolved. How durable this resistance is cannot be predicted.

Any future breeding, whether classical or transgenic, must be aware of the lessons of history when attempting to produce durable resistance to late-blight in potato cultivars. Previously resistant cvs have been overcome quickly and the ability of *P. infestans* to evolve is now potentially greater with the presence of both mating types in most countries where blight is a problem. Fry (2008) states that "any strategy for mitigating pathogenicity needs to be based on a knowledgeable respect for the powerful plasticity of this organism". This "powerful plasticity" remains as much of a challenge as ever.

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