PRACTICAL ASPECTS OF PHENYLAMIDE RESISTANCE MANAGEMENT

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ABSTRACT

Phenylamide resistant (PA) strains of *Phytophthora infestans* were first confirmed in Ireland in 1980 and PA based products were withdrawn from the market. A programme to monitor the distribution of PA resistance confirmed that in the absence of PA based products the distribution of PA resistance decreased rapidly between 1981 and 1983. This apparent lack of fitness was later associated with lower sporangia production per unit leaf-area and the reduced ability to overwinter in tubers stored at low temperatures.

Records of the date of initial outbreak of late blight in unsprayed crops of the cv. "Kerr`s Pink" confirmed that while the average date of outbreak varied between different areas of the country, it was normally after the middle of July. The monitoring programme also confirmed that the distribution of PA resistance was lowest at the beginning of the season and increased thereafter as the season advanced.

Initial experiments on disease control confirmed that there was no significant benefit in using more than 3 sprays of a phenylamide/mancozeb mixture (PAM) in a 10 spray programme based on mancozeb. It was also confirmed that the three systemic sprays were most effective when applied at the beginning of the spraying programme. No further benefit was observed in decreasing the number of systemic sprays below three.

These facts contributed towards the development of an agreed label recommendation which was based on a maximum of 3 early applications of PAMs followed by mancozeb alone to the end of season. This was in conjunction with normal spray intervals and avoiding curative use and use on early potatoes.

Commercial introduction of the PAMs was initially agreed for 1986. However, a severe blight epidemic in early 1985 resulted in the importation and widespread curative use of PAMs in July of that year. Their dramatic effect in controlling the 1985 epidemic when used curatively had a seriously detrimental effect on the official advice for only prophylactic use. A major education programme over a number of years was required before growers were finally convinced of the advantages of following the label recommendations.

INTRODUCTION

Late blight caused by *Phytophthora infestans* (Mont.) de Bary is the most serious disease affecting potatoes in Ireland. Under Irish conditions it has been shown that the disease reaches epidemic proportions in 7 out of 10 years (Cox and Large, 1947). The first systemic fungicide for the control of late blight in potatoes was commercially introduced to Ireland in 1978 in the form of Ridomil 25 WP. The fungicidal activity of this product was based only on the phenylamide (PA), metalaxyl. The early trial results confirmed that metalaxyl was very effective in controlling foliage and tuber blight even at a 21 day spraying interval. The improved control of late blight following the application of metalaxyl led to it`s rapid adoption by growers. By 1980 up to 90% of all potato growers were using the product and over half of this on the cultivar `Kerr`s Pink`. Late in the 1980 growing season control problems were observed in this cultivar. It was confirmed that this was due to a resistant strain of *Phytophthora infestans* (Dowley & O`Sullivan, 1981) and the PA based fungicides were withdrawn from the Irish market. This was the first practical lesson in resistance management showing that effective, long lasting control could not be achieved using the PA alone in a traditional blight control programme.

INITIAL DISTRIBUTION OF PA RESISTANCE

Using the leaf disc test (Staub & Sozzi, 1984), a programme for monitoring the distribution of PA resistance was initiated during the 1981 growing season. This programme confirmed that in the absence of PA based products the distribution of crops with PA resistance present decreased rapidly between 1981 and 1983 (Dowley & O`Sullivan, 1985). This suggested a lack of fitness on the part of the PA resistant strains. Subsequent experiments confirmed that these strains produced fewer sporangia per unit leaf-area than sensitive strains (Dowley, 1987). Further work in Northern Ireland (Walker & Cook, 1990) confirmed that PA resistant strains of *P. infestans* did not survive overwintering at low temperatures in infected tubers as efficiently as sensitive strains. This would suggest that the reduced fitness of resistant strains may be controlled by a number of different genes.

DEVELOPMENT OF AN ANTI-RESISTANCE STRATEGY

Records of the initial date of outbreak of late blight in unsprayed crops of the maincrop cultivar "Kerr`s Pink" confirmed that while the average date of outbreak varied between different parts of the country, it was normally after the middle of July (Frost, 1966). In an average year this would allow 3 sprays of a phenylamide/ mancozeb mixture (PAM) to be applied prior to the first outbreak of late blight. This would also help to reduce the curative use of PAMs.

The resistance monitoring programme also confirmed that there was seasonal variation in the distribution of PA resistance. In each year, the distribution of PA resistance was found to be lowest at the beginning of the season and subsequently increased as the season advanced (Table 1). This was evident for both the period

following the withdrawal of PAs in 1980 and after the commercial reintroduction of the PAMs in 1986.

Initial experiments on disease control confirmed that the best results were obtained from applyinig the PAMs for the first three sprays in the programme and following with mancozeb to the end of the season (Table 2). There was no significant benefit in using more than 3 sprays of a phenylamide/mancozeb mixture (PAM) in a 10 spray programme based on mancozeb and no further benefit was observed in decreasing the number of systemic sprays below three (Table 2). It was also believed that because of increasing maturity, the translocation of metalaxyl became less efficient from the time of flowering to the end of the growing season and therefore should be avoided during this period.

These facts were important in helping the Irish Fungicide Resistance Action Committeee (F.R.A.C.) to formulate an agreed label recommendation for the use of phenylamide/mancozeb mixtures. The main constituents of this recommendation were as follows:-

1. PAMs should be used for the first 3 sprays in the programme
2. Spray interval should not exceed 10 days
3. Subsequent sprays should be with mancozeb alone
4. No PAMs should be used after the end of July
5. PAMs should not be used curatively at any time
6. PAMs should not be used on early potatoes
7. PAMs should not be used on seed potatoes.

INTRODUCTION OF PHENYLAMIDE/MANCOZEB MIXTURES

Commercial introduction of the PAMs was initially agreed for 1986. However, a severe blight epidemic in early 1985 resulted in the importation and widespread curative use of PAMs in July of that year. Their dramatic effect in controlling the 1985 epidemic when used curatively had a seriously detrimental effect on the subsequent prophylactic use PAMs as was officially advised. Following the experience of 1985 the growers were convinced that the PAMs were best used curatively or as a fall back position in the event of poor disease control from the protectant products. This was further aggravated by the much higer price of the systemic type products. Over five years of experience and education was required before growers began to use the PAMs according to the label recommendations (Table 6).

TRIAL RESULTS 1985-`90

Field trials to determine the effects of prophylactic use of PAMs confirmed that when they were used according to the label recommendations they had the effect of delaying the onset of the epidemic, reducing the level of foliage blight at the end of the season, decreasing the incidence of tuber blight and increasing the marketable yield (Table 3). PA resistance was confirmed for all trials sites used from 1985 to 1990.

Information on the levels of foliage blight was also collected from commercial crops through the PA resistance testing programme during the period 1985-`90. This confirmed that where PAMs had been used the level of foliage blight was lower than in crops where a protectant product only was used. Information on fungicide programmes was also collected from crops with no foliage blight present. This showed that the vast majority of crops with no foliage blight had received PAM applications and that these had been applied according to label recommendations.

CURRENT PERFORMANCE OF PAMs

During the period 1991-`93 disease pressure was low but the PAMs have performed well in both field trials and at farm level. In previous years our experience has been that PAMs tended to give their best results in years when the blight epidemics were most severe.

CURRENT DISTRIBUTION OF PA RESISTANCE

The use of phenylamides at farm level from 1986 to 1993 is given in Table 4. In 1986 PAMs were used on nearly all potato crops. In the following years there was a decrease in the use of phenylamides up to 1990 when their use again increased. The PA resistance monitoring programme using the leaf disc method was continued during the period 1986-`93 (Table 5). This confirmed that during the initial years after the introduction of the PAMs there was an increase in the number of crops where PA resistance could be detected (Dowley & O`Sullivan, 1991). This increase in resistance distribution was associated with a high proportion of growers using a phenylamide (Table 4) and also with lack of adherence to the label recommendations. The highest number of crops with PA resistance was detected in 1989 (83%), but the distribution of PA resistance has since fallen steadily.

PAMs are now used on about half the potato crops in the Republic of Ireland and the decrease in the distribution of PA resistance may be associated with the increase in the number of growers who are currently following the recommendations (Table 6).

CURRENT LEVEL OF PA RESISTANCE IN CROPS WITH RESISTANCE

During the three year period 1990-`93 the semi-quantitative (SQ) test has been used to determine the level of PA resistance within crops where PA resistance had been confirmed using the leaf disc test. This revealed that the average level of resistance for each year over this period was slightly in excess of 50% of the population. This fact may explain the superior performance of PAMs in crops where resistance was known to occur.

Continued resistance monitoring and field trials are necessary to confirm the continued advantages of the phenylamide/mancozeb mixtures for blight control in Ireland.

TABLE 1. Seasonal variation in the distribution of PA resistance in the Republic of Ireland.

	% Crops with PA resistance	
Month	1981-`85	1986-`93
June	0.5	16.6
July	5.0	54.8
August	20.0	63.7
September	24.7	52.9
Number of crops surveyed	281	1,167

TABLE 2: Comparison of different phenylamide based strategies on foliage and tuber blight (Oak Park, Carlow, 1985)

Treatment	% Foliage Blight (end of season)	Tuber Blight (t/ha)
Unsprayed	100	0.13
Mancozeb all season	46	0.21
PMM 2nd & 3rd spray	28	0.05
PMM 1st spray	26	0.02
PMM 2nd spray	23	0.13
PMM 3rd spray	31	0.07
PMM All Season	29	0.02
PMM 1st, 2nd & 3rd spray	19	0.00
LSD (5%)	27	0.12

Table 3: Effect of phenylamides on late blight control in Ireland. (Mean of National Blight Trial, Carlow, 1985-`90)

Treatment	Delay (days) in Disease Onset	% Foliage Blight end of Season	Yield in t/ha	Tuber Blight t/ha
Unsprayed	0.0	95.6	34.69	0.44
Mancozeb	9.8	36.7	42.50	0.24
Galben M	14.3	34.3	44.31	0.14
Ripost	21.5	18.4	46.93	0.07
Ridomil MZ 72	21.7	16.7	46.63	0.09

TABLE 4: Annual use of phenylamides in Ireland (Resistance monitoring programme).

Year	No. crops Sampled	% Crops on which used
1986	104	100
1987	97	92
1988	68	72
1989	23	43
1990	50	38
1991	40	42
1992	43	39
1993	49	51

TABLE 5: Frequency of PA resistance in the Republic of Ireland 1986-`93

Year	No crops with late blight	% Crops with resistance
1986	92	29
1987	88	76
1988	66	83
1989	23	83
1990	48	56
1991	37	46
1992	38	45
1993	45	64

TABLE 6: Date of application of first phenylamide spray

Year	Sample Size	% growers applying first spray before		
		June 16	June 25	June 30
1990	12	0	8	25
1991	13	0	8	39
1992	14	21	50	57
1993	23	26	52	74

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VARIATION FOR RESPONSE TO PHENYLAMIDES IN UK POPULATIONS OF *BREMIA LACTUCAE* (LETTUCE DOWNY MILDEW) AND *PERONOSPORA PARASITICA* (BRASSICA DOWNY MILDEW)

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ABSTRACT

Failure to control downy mildew of horticultural brassicas and lettuce due to phenylamide insensitivity was first reported in the UK in 1983. In both cases, there was evidence that a single insensitive clone was rapidly disseminated throughout production regions with transplanting material. The insensitive population of *Peronospora parasitica* appeared to have become phenotypically more diverse a few years later. Over a 10 year period, there have been cycles of increase and decline in three different phenylamide insensitive pathotypes of *Bremia lactucae* that became prevalent among the 12 that have been characterised. Decline has always been associated with widespread adoption of an integrated control strategy involving the deployment of cultivars carrying resistance genes against which the prevalent insensitive pathotype was avirulent.

INTRODUCTION

Downy mildews of cruciferous vegetables (caused by *Peronospora parasitica*) and lettuce (caused by *Bremia lactucae*) are economically damaging diseases in the UK and most other important production regions throughout the world (Channon, 1981; Crute, 1992a). During young plant propagation, both diseases can result in serious crop losses and a high level of control is demanded. Subsequently, disease in the mature crop adversely affects quality and may in extreme circumstances, lead to complete loss of marketable yield.

Exceptionally effective control of these diseases became possible in the late 1970s following the introduction of phenylamide fungicides, and in particular, products containing metalaxyl. However, in the UK, the high selection pressure imposed by sustained and frequent use of fungicides containing metalaxyl resulted in the emergence of pathogen variants with a high level of insensitivity 5 years after initial commercial use (Crute *et al.*, 1985). Field control failures due to insensitivity were subsequently reported from other countries (Table 1).

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TABLE 1. Reports of phenylamide insensitivity in *B. lactucae* and *P. parasitica*.

Year	*Bl*	*Pp*	Reference
1983	UK	UK	Crute *et al.*, 1985
1987	France		Leroux *et al.*, 1988
	California, USA		Schettini *et al.*, 1991
1989	Florida, USA		Raid *et al.*, 1990

Bl = Bremia lactucae; *Pp = Peronospora parasitica*

Circumstances associated with the initial failure to control *B. lactucae* with phenylamide fungicides in UK production have been fully documented elsewhere (Crute, 1987; Crute *et al.*, 1987) as have details of an effective integrated control strategy based on continued fungicide use in combination with cultivars carrying an appropriate downy mildew resistance gene (*Dm* genes) or gene combination (McPherson & Crute, 1986; Crute, 1987; Crute 1992a, 1992b, 1992c). This paper provides an up-dated summary of studies conducted over a 10 year period on variation in the UK population of *B. lactucae* with respect to cultivar specific virulence, sensitivity to metalaxyl and sexual compatibility type (SCT).

Studies on the occurrence and distribution of phenylamide insensitive variants of *P. parasitica* associated with control failure in UK production of horticultural brassicas (all forms of *Brassica oleracea*) have not previously been documented. This paper provides information from studies conducted between 1983 and 1985, soon after the initial discovery of phenylamide insensitivity, together with further information gathered a few years later in 1989.

MATERIALS AND METHODS

A single mass-spore pathogen culture was derived from each disease sample obtained using methods previously described for the establishment and maintenance of *P. parasitica* and *B. lactucae* (Crute *et al.*, 1985, 1987; Moss *et al.*, 1994). All samples were obtained from crops being grown commercially in the UK.

Methods for determination of cultivar specific virulence and SCT type were as described fully elsewhere (Michelmore & Crute, 1982; Crute *et al.*, 1987; Moss *et al.*, 1994). The response of pathogen isolates to phenylamide fungicides was assayed on fungicide treated seedlings grown and inoculated under controlled conditions. Full details of the methods employed have been published previously (Crute *et al.*, 1985; Crute, 1987; Moss *et al.*, 1994). Variation for fungicide sensitivity was described by the incidence of sporulation and the time taken for it to occur on a batch of inoculated seedlings treated with a range of fungicide concentrations. Standard control isolates with a known response to fungicide were included in all assays. For each batch of treated seedlings, a value for the mean reciprocal latent period (time in days from inoculation to sporulation; 1/LP) was calculated and expressed as a percentage of this value obtained following inoculation of untreated seedlings. Reciprocals were used to

allow seedlings on which the fungus did not sporulate to be readily included in calculations (1/LP = 0). On this basis, isolates that were completely insensitive to a particular concentration of fungicide had values close to 100 while those that were completely sensitive had values close to 0. A few isolates of both *P. parasitica* and *B. lactucae* consistently expressed differing degrees of intermediate response as indicated by values between these extremes. Isolates thought to be heterozygous at a locus (*P*) controlling response to phenylamide fungicides have previously been shown to exhibit an intermediate response phenotype (Crute & Harrison, 1988; Moss *et al.*, 1994).

RESULTS

Peronospora parasitica

Isolates of *P. parasitica* highly insensitive to phenylamide fungicides were first obtained from Lincolnshire, UK in 1983; a commercial propagator of brassica plants experienced failure to control the disease with metalaxyl. Subsequently, insensitive isolates were recovered from mature crops in the same region (Crute *et al.*, 1985). During 1984 metalaxyl insensitive isolates of the pathogen were also recovered from crops in Norfolk, Lancashire, Cambridgeshire, Cheshire, Worcestershire, Fife, Mid-Lothian and Borders. During 1985, phenylamide insensitive isolates from Jersey, Kent and Cardigan were also recovered. There was circumstantial evidence that a phenylamide insensitive pathotype had been rapidly disseminated with module-raised plants from which transplanted crops were produced. During 1985, 16 brassica propagation sites in Lincolnshire were surveyed between March and June for incidence of downy mildew; isolates obtained from sites where mildew was present were assayed for response to metalaxyl (Table 2). By April, there was downy mildew present at most sites and in excess of 60% of sites yielded insensitive isolates. This confirmed the prevalence of the problem and the conjecture that planting material provided an efficient means for dispersal of the pathogen.

TABLE 2. Incidence and response to metalaxyl of *P. parasitica* at 16 brassica propagation sites in Lincolnshire, UK (March - June 1985).

	March	April	May	June
Incidence[a]	38	56	50	63
Response to metalaxyl[b]	67	67	63	80

[a] Percentage of sites (sample size = 16) from which a viable sample of *P. parasitica* was obtained for testing.

[b] Percentage of those sites from which a viable *P. parasitica* sample was obtained where metalaxyl insensitivity was confirmed.

An interesting characteristic observed for the standard phenylamide

insensitive isolate studied (referred to as P006) was the lack of complete cross-insensitivity between metalaxyl and cyprofuram (Table 3) (Crute *et al*, 1985; Moss *et al.*, 1994). While the standard sensitive isolate (referred to as P005) was more sensitive to metalaxyl than cyprofuram, the opposite was the case for isolate P006. Cyprofuram retained significant activity at 10 μg/ml in assays of P006 while metalaxyl exerted no control at this concentration and exhibited little activity at 100 μg/ml. Isolate P006 was also shown to be of P2 SCT and was virulent on the a land-race cauliflower (Palermo Green) previously identified as expressing isolate specific resistance to *P. parasitica*.

Subsequently, 13 isolates from seven counties obtained during 1983-1985 were tested for SCT, virulence on Palermo Green and response to metalaxyl and cyprofuram. All 13 isolates were phenotypically identical to P0583 which strongly suggests that a single pathotype of clonal origin had become widely distributed during this period.

TABLE 3. Differential response of *P. parasitica* to metalaxyl and cyprofuram.

	μg/ml				
Isolate	0.01	0.1	1.0	10.0	100.0
P005 Metalaxyl	85[a]	0	0	0	0
P006	107	106	105	101	80
P005 Cyprofuram	109	84	2	0	0
P006	99	99	101	5	0

[a] Values are 1/LP as a % of untreated

In 1989, a small sample of seven phenylamide insensitive isolates was obtained from Lincolnshire and these were also subjected to phenotypic characterisation for SCT, virulence on Palermo Green and response to metalaxyl and cyprofuram (Table 4). Interestingly, five different phenotypes were evident among the seven isolates. Two isolates were identical to those derived from the 1983/85 sample indicating that the original clone was probably still prevalent in the population. Isolates avirulent on Palermo Green, either homothallic or of P1 SCT and not exhibiting differential sensitivity between cyprofuram and metalaxyl were represented among the other five isolates. This diversity of phenotypes is indicative of either sexual recombination or the selection, since 1983, of novel phenylamide insensitive mutants.

TABLE 4. Phenotypic characteristics of seven phenylamide insensitive isolates of *P. parasitica* obtained from Lincolnshire in 1989.

Phenylamide response	F(M>C)	I(M=C)	F(M=C)	F(M>C)	F(M>C)
"Palermo Green"	V	V	nt	V	A
SCT	P2	P1	nt	H	H
Number of isolates	2	1	1	2	1

V = virulent; A = avirulent; H = homothallic
F = fully insensitive; I = intermediate;
M>C = differential response to metalaxyl and cyprofuram (see Table 3);
M=C = equivalent response to metalaxyl and cyprofuram

Bremia lactucae

In a continuing study of variation within the UK population, over 520 isolates of *B. lactucae* have been assayed since 1983 for cultivar specific virulence, SCT and response to metalaxyl. Over this period, 12 phenotypically distinct metalaxyl insensitive pathotypes have been identified (Table 5) of which three have sequentially become widespread and caused significant problems for UK lettuce producers. While several of these pathotypes are fully insensitive, others express differing levels of intermediate sensitivity (Table 5). During 1992 and 1993, a pathotype of intermediate insensitivity, referred to as "1992A", became prevalent in several UK lettuce production regions. This indicates that field control failure is not necessarily always associated with the occurrence of isolates fully insensitive to phenylamide fungicides, an observation borne out by similar experiences in California (Schettini *et al.*, 1991).

A pathotype referred to as the "NL10 type" caused the initial failure of metalaxyl to control lettuce downy mildew; this pathotype was first located in Lancashire and between 1983 and 1986 it became distributed to all lettuce production regions in the UK (Crute *et al.*, 1987) (Table 6). Isolates of the "NL10 type" have not been recovered since 1988 when a single sample from Northern Ireland proved to be of this pathotype. The decline of the "NL10 type" was associated with encouragement to grow cultivars of lettuce carrying *Dm11* on which this pathotype is avirulent (Table 5). In 1987 the first occurrences of an insensitive pathotype referred to as the "NL15 type" were recorded; this pathotype was virulent on cultivars carrying *Dm11* (Table 5) and rapidly became prevalent throughout lettuce production regions during 1988 and 1989 (Table 6). The "NL15 type" was countered by encouragement to grow cultivars carrying either *Dm6* or *Dm16* on which it was avirulent. A phenylamide insensitive pathotype identical to the "NL15 type" was also reported to be prevalent in France during 1987/88 (Leroux *et al.*, 1988). Only a few isolates of this pathotype have been recovered from UK crops each year since 1990 indicative of the success of the control strategy. In 1992 several new insensitive pathotypes were identified mostly virulent on cultivars carrying *Dm16* which were by this time being favoured by growers. Of these new pathotypes, one,

referred to as "1992A", has predominated (Table 6). This pathotype is avirulent on cultivars carrying *Dm3* and *Dm6* and it should therefore be possible readily to counteract it by choice of appropriate cultivars.

TABLE 5. Characteristics of 12 metalaxyl insensitive pathotypes of *Bremia lactucae* from UK lettuce crops.

Pathotype Name	Years Found	Metalaxyl Response	Virulence/avirulence *Dm*: 3	6	11	16	18	SCT	Distribution
NL10	83-88	103[a]	+	+	-	-	-	B2	Widespread
86A	86	67	-	-	+	-	-	B1	Limited
NL15	87-92	105	+	-	+	-	-	B1	Widespread
87A	87	64	-	+	-	-	-	nt	Limited
87B	87	10	+	+	-	+	-	B2	Limited
89A	89	102	+	+	+	-	-	B2	Limited
89B	89+93	45	+	+	+	-	-	B1	Limited
92A	92-93	82	-	-	+	+	-	B2	Widespread
92B	92	102	+	+	+	-	-	H	Limited
92NI	92	93	+	-	(+)	+	-	B1	Limited
NL16	92	82	+	+	+	+	-	B1	Limited
92C	92	94	+	-	+	+	-	nt	Limited

[a] Values are 1/LP as a % of untreated; nt = not tested
+ = virulent; - = avirulent; (+) = partially virulent;
Dm = Downy mildew resistance gene.

TABLE 6. Incidence of occurrence of *B. lactucae* pathotypes among 522 isolates tested from 1983-1993.

		Pathotype Name												
Year	N[a]	NL10	86A	NL15	87A	87B	89A	89B	92A	92B	92NI	NL16	92C	SEN[b]
83	33	17												16
84	50	28												22
85	133	94												39
86	39	20	2											17
87	34	4		3	1	1								25
88	96	1		79										17
89	44			24			1	1						18
90	12			8										4
91	8			2										6
92	36			3					22	1	2	4	1	3
93	36			1				2	25					8
Tot	522	164	2	120	1	1	1	3	47	1	2	4	1	175

[a] Number of isolates tested; [b] All sensitive pathotypes

As illustrated in Table 6, since 1983, there have been three cycles of rapid increase and decline in three different phenylamide insensitive

pathotypes of *B. lactucae*. There is little reason to doubt that rapid dissemination from the original area where a new pathotype emerges is associated with the movement of transplanting material. The first two pathotypes to become prevalent were countered by encouragement to grow appropriately resistant cultivars while continuing the use of fungicides containing metalaxyl to control virulent but sensitive components of the pathogen population. It remains to be seen how long this dynamic integrated control strategy can be successfully maintained but there are good prospects that the recently emerged "1992A" type can be similarly controlled once cultivars carrying the required *Dm* genes have been identified.

DISCUSSION

The studies reported in this paper clearly illustrate the impact of modern horticultural production practices on the rapid dissemination of new pathogen variants including those insensitive to fungicides. These observations assume a particular relevance with the deregulation of trade in plant material throughout countries of the European Union. These investigations have provided some important insights into pathogen population biology and have led to a successful strategy for lettuce downy mildew control and the continued effective use of phenylamide fungicides. However, several important biological questions remain to be answered.

What is the relative importance of sexual recombination and selection of novel mutants as the origins of new pathotypes?

How many genetic loci control response to phenylamides and is the observed phenotypic variation related to allelic variation?

Is it chance, or are there important phenotypic characters which determine if a new pathotype will become widespread or remain of limited commercial significance?

The answers to these questions are likely to emerge from inheritance and population studies employing techniques to identify selectively neutral DNA-based genetic markers.

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