

Factors affecting build-up of fungicide resistance in powdery mildew in spring barley

K.J. BRENT¹, G.A. CARTER¹, D.W. HOLLomon¹, T. HUNTER¹, T. LOCKE² and M. PROVEN³

¹ Department of Agricultural Sciences, University of Bristol, AFRC Institute of Arable Crop Research, Long Ashton Research Station, Bristol, BS18 9AF, UK

² ADAS Area Laboratory, Kings Road, Evesham, Worcestershire, WR11 5BE, UK

³ Drayton Experimental Husbandry Farm, Alcester Road, Stratford-upon-Avon, Warwickshire, CV37 9RQ, UK

Accepted 11 May 1989

Abstract

In replicate-plot field experiments done in the UK, at one site in Avon for 3 years and another in Warwickshire for 2 years, application of ethirimol or triadimenol sprays or seed treatments was followed by decreases in sensitivity of mildew samples to the particular fungicide applied. Application of ethirimol-triadimenol or tridemorph-triadimenol mixtures caused smaller or no decreases in sensitivity. Differences between isolates in responses to ethirimol and to triadimenol treatment were usually negatively correlated. Early-season inoculum differed in fungicide sensitivity between sites. At one site sensitivity shifted markedly from one season to another. No clear interactions between cultivar, mildew pathotype and shifts in fungicide response could be discerned. There were no major differences in resistance build-up between seed or spray treatments.

Additional keywords: ethirimol, triadimenol, tridemorph, *Erysiphe graminis* f. sp. *hordei*

Introduction

Widespread use of fungicides inhibiting the 14-C demethylation step in sterol biosynthesis (DMIs) to control barley powdery mildew *Erysiphe graminis* f. sp. *hordei*, has been accompanied in the UK by a decrease in sensitivity of mildew to these fungicides (Fletcher and Wolfe, 1981; Butters et al., 1984). Change has been gradual, involving replacement in certain regions, of the wild-type heterogeneous population with an overlapping population, still heterogeneous but with a lower mean sensitivity. This contrasts with the pattern of selection observed in some other fungicide resistance situations, where an entirely distinct resistant population quickly, and completely, replaced the wild-type sensitive forms (Skylakakis, 1985). Several mathematical models have been developed which predict the likely outcome of different fungicide strategies on the spread of resistance. Each model embodies different assumptions, but general conclusions are similar in indicating that mixtures, or alternating sequences, of fungicides which are not related by cross-resistance will restrict the spread of resistance (Skylakakis, 1982). Few attempts have been made to validate these models experimentally. There is limited evidence to suggest that mixtures do delay the spread

of phenylamide resistance in *Phytophthora infestans* (Staub and Sozzi, 1983) and *Pythium* (Sanders et al., 1985), and MBC resistance in *Pseudocercospora herpotrichoides* (Hoare et al., 1986).

None of these models analyses the situation found in barley powdery mildew, where the gradual decline in sensitivity to 2-aminopyrimidine and triazole fungicides probably reflects the selection of several resistance genes (Hollomon, 1981; Brent, 1982; Hollomon et al., 1984). Although attempts have recently been made to develop models that describe the evolution of polygenically controlled fungicide resistance (Shaw, 1989; Josepovits, 1989), effective strategies for delaying the build-up of resistance to these two types of fungicide in barley mildew can only be derived, at present, from field experimentation. Alternating sequences of triazole fungicides with either an aminopyrimidine or morpholine, had little influence on the spread of triazole resistance at one UK field site in Bedfordshire (Butters et al., 1983). Field experiments at Long Ashton on a mildew-susceptible cultivar, Golden Promise, suggested that use of mixtures of a triazole fungicide with ethirimol delayed development of resistance to both these fungicides (Hunter et al., 1984), and similar findings for propiconazole and tridemorph have emerged from field studies reported by Bolton and Smith (1988). The present report extends the evaluation of mixtures to include three different cultivars, a factor which may also influence the spread of resistance (Wolfe and Dinoro, 1973; Wolfe et al., 1983; Butters et al., 1984).

Materials and methods

Two similar field experiments were carried out in 1984 and 1985, at Long Ashton Research Station, near Bristol, and also ca. 100 km north at Drayton Experimental Husbandry Farm, near Stratford-upon-Avon. An additional experiment in 1987 at Long Ashton, using only one cultivar, Golden Promise, explored further the value of triadimenol-tridemorph mixtures applied as sprays.

Randomized block designs were used at both sites, incorporating plots of 12 × 12 m at Long Ashton, and 12 × 13 m at Drayton. At Long Ashton the experiments were done on the same site each year, but involved some different treatments (Table 1) in the three years. At Drayton, the same treatments and the same randomized design were used in both years, but the two successive experiments were conducted in fields 500 m apart. Three barley cultivars, Golden Promise, Triumph and Patty, which differ in their susceptibility to mildew, were grown at both sites.

Amounts of field mildew were assessed on a sample of 10 random tillers per plot at appropriate intervals, either as numbers of active pustules per leaf or as percentage leaf area infected.

Two techniques were used to assay sensitivity of mildew to triadimenol and ethirimol. A 'bait plant' method was based on barley seedlings (cv. Golden Promise) grown in pots in a controlled-environment facility from seed treated with either fungicide at five rates (Hunter et al., 1984). The seedlings were exposed within field plots (3-4 days), just before the first spray was applied, and 2 weeks after each fungicide spray. Pustules developing at each seed-applied dose were counted after 7 days incubation in a greenhouse. Fungicide sensitivity was expressed as the dose (in terms of g active ingredient per 100 kg of seed) needed to reduce pustule numbers to half the number present on untreated seedlings (ED₅₀). Suitable statistical analyses

Table 1. Field experiment information.

	Drayton		Long Ashton		
	1984	1985	1984	1985	1987
Sowing date:	3 April	12 March	9 March	12 March	13 March
Spray dates:	31 May	14 June	14 May	17 May	20 May
	11 June	30 June	4 June	14 June	18 June
Mildew samples collected:	25 May	5 June	11 May	10 May	18 May
	25 June	28 June	31 May	31 May	5 June
		18 July	1 July	10 July	29 June

Cultivars: Golden Promise, Triumph, Patty; *Replicates:* four; *Design:* randomized block.

Fungicides: Triadimenol as Baytan seed treatment or as Bayfidan spray; Ethirimol as Milstem seed treatment or as Milgo E spray; Triadimenol/ethirimol mixture as Bayfidan plus Milgo E tank mix, or as Ferrax seed treatment; Triadimenol/tridemorph mixture as Dorin; All fungicides used at manufacturers' recommended rates.

were applied to correct for the different infection levels on untreated seedlings exposed in different plots (Hunter et al., 1984).

Leaf segment assays were made in the laboratory on mildew samples taken from 25 diseased leaves collected at random from each field plot, and allowed to sporulate overnight before use. Mildew samples were collected during the period that 'bait plants' were exposed in field plots. Ethirimol assays were based on appressoria formation as described by Hollomon (1977), and triadimenol assays on measurements of colony growth (Hollomon, 1982). In each case leaf segments were floated on solutions containing four different fungicide concentrations. A standard sensitive isolate was included in all triadimenol assays, and ED_{50} values (given in terms of μg fungicide ml^{-1}) adjusted according to differences that occurred between tests with this isolate. Technical grade triadimenol and ethirimol were used in both laboratory assays, and were kindly supplied by their respective manufacturers, Bayer (UK) Ltd. and ICI Agrochemicals Plc.

Results

Fungicide sensitivity. Treatment with either triadimenol or ethirimol alone, was found at both sites to decrease sensitivity, as measured by both assay methods, to the particular fungicide applied (Table 2). Changes in ethirimol sensitivity were generally more pronounced than changes in triazole sensitivity. Mixing either tridemorph or ethirimol in foliar sprays with triadimenol (all at commercially recommended rates), limited decline in triazole sensitivity at both sites, especially in 1985 and 1987. Likewise, use of a mixture of ethirimol and triadimenol limited spread of ethirimol resistance at Drayton. Treatment with ethirimol alone actually increased triazole sensitivity, particularly at Drayton, whilst treatment with triadimenol alone often increased ethirimol sensitivity. There was no clear evidence that seed treatment formulations of either fungicide provided any greater or smaller selection pressures, than did subsequent spray treatments.

Table 2. Effects of different spray programmes on fungicide sensitivity in barley powdery mildew.

Strategy	Fungicide sensitivity (ED ₅₀)								
	Drayton				Long Ashton				
	1984		1985		1984		1985		1987
	BP	LS	BP	LS	BP	BP	LS	LS	
	<i>Triadimenol</i>								
No fungicide	20a	0.5a	103a	1.9a	18a	22a	0.6a	0.8a	
Triadimenol	42b	1.7b	310b	2.2a	41b	54b	2.4b	4.9b	
Ethirimol	17a	0.2a	43c	1.4b	20a	20a	0.3ac	NT	
Triadimenol/Ethirimol	22a	1.4b	76ac	1.4b	NT	NT	NT	NT	
Triadimenol/Tridemorph	NT	NT	NT	NT	NT	16a	0.8a	1.2a	
	<i>Ethirimol</i>								
No fungicide	293a	1.0a	111a	0.6a	273a	215a	1.7a	1.8a	
Triadimenol	136b	2.0b	79a	0.5a	190a	175a	*	1.3b	
Ethirimol	4000c	9.6c	216b	1.9b	4000b	591b	5.5b	NT	
Triadimenol/Ethirimol	156ab	3.0b	128a	0.5a	NT	NT	NT	1.2a	
Triadimenol/Tridemorph	NT	NT	NT	NT	NT	99c	*	NT	

BP = Bait plant technique. Sensitivity expressed as ED₅₀ (g a.i./100 kg seed).

LS = Laboratory technique. Sensitivity expressed as ED₅₀ (µg/ml).

* = Assay not conducted because insufficient mildew was available from plots.

NT = Treatments not included.

Samples taken after last spray, except for ethirimol assays at Long Ashton in 1987, which were conducted on mildew collected before the first spray. Values in each column followed by the same letter have non-overlapping 95% confidence limits. These significance values do not apply across the rows.

Mildew from the cultivar Triumph was generally more sensitive to both fungicides regardless of treatment (Table 3), than was mildew from Golden Promise. The sensitivity of mildew from Patty frequently lay between these two extremes. However, these differences in sensitivity were often small, and no significant interactions between cultivars and the response of the mildew developing on them to the different fungicide treatments, either in the field or in bioassays, were apparent.

At Long Ashton, the sensitivity of barley mildew to each fungicide hardly changed between 1984 and 1987 (Table 2). Whilst in 1984 there was little difference between the two sites, by 1985 the mildew population at Drayton was clearly less sensitive to triadimenol, yet more sensitive to ethirimol than that at Long Ashton. Assays conducted during the early stages of the 1985 epidemic at Drayton, showed significant changes in sensitivity of mildew, compared to the last assays conducted there in 1984 (Table 4), suggesting that the 1985 inoculum did not derive predominantly from the mildew population present on the same untreated plots in the previous July.

Table 3. Effect of cultivar on fungicide sensitivity.

Cultivar	Fungicide sensitivity (ED ₅₀)						
	Drayton				Long Ashton		
	1984		1985		1984	1985	
	BP	LS	BP	LS	BP	BP	LS
	Triadimenol						
Golden Promise	34a	0.5a	197a	2.1a	20a	34a	0.5a
Triumph	21a	0.03b	101b	1.4b	19a	24a	0.5a
Patty	25a	0.3a	100b	1.6ab	33a	25a	0.7a
	Ethirimol						
Golden Promise	232a	3.8a	141a	1.0a	208a	342a	3.2a
Triumph	179a	1.5b	114a	0.8ab	140a	252ab	0.3b
Patty	202a	1.7b	113a	0.4b	244a	216b	1.8c

For abbreviations see Table 2.

Values are from samples collected after the last spray, and are means for all fungicide treatments. For each fungicide, values followed by the same letter in each column have overlapping 95% confidence limits.

Table 4. Fungicide sensitivity in mildew from untreated plots at Drayton.

Fungicide sensitivity (ED ₅₀)	Triadimenol		Ethirimol	
	BP	LS	BP	LS
	Last assay; 1984	20a	0.5a	293a
First assay; 1985	41b	1.5b	75a	0.6b

For abbreviations see Table 2.

Values are the means for all three cultivars, but for untreated plots only. For each fungicide, values followed by the same letter in each column have overlapping 95% confidence limits.

Disease control. In 1985 crop growth was delayed as a result of late sowing. The mildew epidemic also began late, but subsequently reached levels similar to those encountered in 1984. At both sites there was little evidence of an interaction between fungicides and cultivars in terms of mildew control in either year. Throughout, the amount of mildew on Patty and Triumph was less than in Golden Promise, in untreated and treated plots.

In 1984 all fungicide strategies performed well at both sites, although as expected, ethirimol sprays (Milgo E) were generally less effective than the triadimenol spray

Table 5. Fungicide use and mildew levels at Drayton in 1984 and 1985.

Seed treatment	Sprays ($\times 2$)	Percentage leaf area infected		
		23 May 1984	6 June 1984	27 June 1984
None	None	21.0 (-1.10)	4.6 (-2.95)	32.0 (-0.39)
None	Triadimenol	-	1.9 (-3.70)	1.9 (-3.70)
None	Triadimenol/Ethirimol	-	0.8 (-4.28)	0.2 (-4.90)
Triadimenol	Triadimenol	7.3 (-2.48)	0.6 (-4.50)	1.1 (-4.04)
Ethirimol	Ethirimol	2.8 (-3.30)	0.6 (-4.50)	2.6 (-3.45)
LSD 5%		(0.22)	(0.28)	(0.30)

Seed treatment	Sprays ($\times 2$)	Percentage leaf area infected		
		5 June 1985	28 June 1985	18 July 1985
None	None	7.2 (-2.54)	4.8 (-2.35)	80 (1.75)
None	Triadimenol	-	1.4 (-3.94)	70 (1.26)
None	Triadimenol/Ethirimol	-	1.2 (-4.02)	29 (-0.88)
Triadimenol	Triadimenol	2.3 (-3.56)	1.1 (-4.04)	68 (1.00)
Ethirimol	Ethirimol	0.7 (-4.40)	0.7 (-4.43)	64 (0.50)
LSD 5%		(0.24)	(0.36)	(0.40)

Data were subject to analysis of variance after transformation of values to logits ($\log_e [(0.5 + \text{Data})/(100.5 - \text{Data})]$). Figures in brackets are these logit values.

Values for 23 May 1984 and 5 June 1985 are the means of infection on leaves 3 and 4 of cv. Golden Promise.

Values for 6 June 1984 and 28 June 1985 are the means of infection on leaves 2 and 3 of cv. Golden Promise.

Values for 27 June 1984 and 18 July 1985 are the means of infection on leaves 1 and 2 of cv. Golden Promise.

(Bayfidan). On all cultivars triadimenol seed treatment (Baytan) improved the degree of disease control achieved by subsequent triadimenol sprays. The triadimenol/ethirimol spray mixture performed only slightly better than either fungicide applied alone. A commercial mixture of triadimenol and tridemorph (Dorin) also performed well at Long Ashton in 1987.

In 1985 different patterns of mildew control emerged at Drayton, where continuous use of triadimenol was less satisfactory. Triadimenol seed treatment still enhanced the effectiveness of subsequent triadimenol sprays. Ethirimol seed treatment performed significantly better than triadimenol seed treatment on Patty and Golden Promise, but not on Triumph. The spray mixture of triadimenol plus ethirimol now gave the best mildew control in 1985 on 'Golden Promise' (Table 5).

Yield. In 1984, substantial yield increases were obtained with all fungicides at both sites (Table 6). At Long Ashton, Triumph yielded best, and no major interactions bet-

Table 6. Effect of different fungicide treatments on barley yield.

Treatment	Yield (tonnes 85% dry matter ha ⁻¹)				
	Drayton		Long Ashton		
	1984	1985	1984	1985	1987
<i>Golden Promise</i>					
None	4.0	3.4	4.4	3.8	5.0
Triadimenol	4.9	3.3	5.6	5.5	5.5
Ethirimol	5.3	3.4	5.4	4.2	NT
Triadimenol/Ethirimol	5.8	3.8	NT	NT	NT
Triadimenol/Tridemorph	NT	NT	NT	5.8	5.9
<i>Triumph</i>					
None	4.8	4.3	5.1	4.3	NT
Triadimenol	6.2	4.6	6.0	6.5	NT
Ethirimol	6.0	5.3	6.1	5.4	NT
Triadimenol/Ethirimol	6.4	4.5	NT	NT	NT
Triadimenol/Tridemorph	NT	NT	NT	6.3	NT
<i>Patty</i>					
None	5.3	6.0	4.7	3.8	NT
Triadimenol	6.2	5.7	5.9	5.2	NT
Ethirimol	6.2	5.1	5.6	5.1	NT
Triadimenol/Ethirimol	5.7	6.2	NT	NT	NT
Triadimenol/Tridemorph	NT	NT	NT	5.1	NT
LSD 5%	1.0	1.1	0.8	0.9	0.9

NT = No treatment.

ween cultivars and fungicides were observed. Without fungicides Patty yielded best at Drayton, but did not respond so well as the other two cultivars to fungicides. All fungicide strategies again increased yields at Long Ashton in 1985, but not at Drayton where even the triadimenol/ethirimol spray mixture gave only small increases. The triadimenol/tridemorph mixture used at Long Ashton in 1987 gave apparently larger yield increases than triadimenol alone.

Discussion

Both assay methods detected seasonal changes in sensitivity to triadimenol and ethirimol in mildew sampled from plots treated with the respective fungicide, indicating that 12 × 12 m plots are of sufficient size to allow detection of the effects of different fungicide strategies. However, assays were conducted on too few occasions in any one year to determine exactly what relationship might exist between fungicide selection and the rate of change in ED₅₀ during the course of the mildew epidemic. At Long Ashton, the sensitivity of mildew to triadimenol at the start of epidemics in all three years, was little different from that observed before 1984 (Hunter et al., 1984).

Yet where triadimenol was applied, mildew within those plots always became less sensitive to this fungicide during the year. As these effects of selection did not accumulate in the following year, it seems likely that the mildew epidemic in 1985 was initiated with inoculum originating predominantly from outside the site, and which was again sensitive to triadimenol. Alternatively, the proportion of resistant forms may have decreased markedly through lack of fitness. The situation at Drayton was somewhat different. Triadimenol sensitivity declined slightly in 1984 where this fungicide was applied alone. When mildew was first assayed in early June at the start of the 1985 epidemic, triadimenol sensitivity had declined much further, even in mildew from untreated plots. This suggests that with a mobile pathogen such as powdery mildew, the sensitivity to fungicides of the inoculum initiating epidemics can differ significantly between years at different sites, and this will influence the outcome of different fungicide strategies. At this stage it is not clear what measurements must be made in order to incorporate ingress information into mathematical models such as that developed by Shaw (1989), and which might predict the effects of different fungicide treatments on the development of fungicide resistance. Especially towards the end of the epidemic, mildew control was worse than in the previous year (Table 5). Overall disease levels were also lower in 1984, but this was due entirely to less infection on Triumph and Patty. Many factors may contribute to these changes in the performance of triazoles, but they are linked to changes in triazole resistance levels.

These experiments also demonstrate that use of certain fungicide mixtures do slow down the development of resistance to triadimenol or ethirimol, and provide worthwhile disease control and yield benefits. This extends the generally similar findings of Hunter et al. (1984) and of Bolton and Smith (1988); some of the present data have been quoted by Heaney et al. (1988). Where fungicide resistance is controlled by a single gene exerting a large effect, fungicide mixtures appear to be ineffective in preventing a further build-up once resistance can be detected readily in the field. However, mixtures based on DMIs or ethirimol were beneficial when applied to cereal powdery mildews, even after a significant decrease in sensitivity and performance was detected. Furthermore, mixtures of fungicides appear preferable to alternating sequences; these were found in other field experiments to have little effect on triadimenol sensitivity (Butters et al., 1983; Bolton and Smith, 1988), although over large areas alternation may be more successful.

Selection with triadimenol increased the sensitivity of mildew samples to ethirimol, whilst selection with ethirimol increased triadimenol sensitivity, especially at Drayton. Similar changes have been observed in earlier experiments (Hunter et al., 1984; Hollomon et al., 1985). Furthermore, the overall decline in triadimenol sensitivity observed at Drayton between 1984 and 1985 was accompanied by a significant increase in sensitivity to ethirimol. Although these converse changes in sensitivity to ethirimol and triadimenol may enhance the benefits of mixtures containing these two fungicides, the biochemical, genetic or epidemiological basis of the negatively correlated response remains unclear. Isolates showing decreased sensitivity to triadimenol are frequently very sensitive to ethirimol (Butters et al., 1983). Whilst isolates resistant to both fungicides have been detected in field populations (Hollomon, unpublished observation), their fitness has not yet been examined. Converse responses between triadimenol and tridemorph have not been observed in barley powdery mildew (Hollomon, 1982), and the benefits of a mixture containing these two fungicides can-

not be explained in these terms.

Cultivar is another factor which may influence sensitivity of mildew to fungicides (Wolfe and Dinooor, 1973; Wolfe et al., 1983; Butters et al., 1984). Thus mildew isolates collected in the UK before 1984, and which were able to infect cultivars such as Wing and Triumph that contain the *Mla7* host resistance gene, were more sensitive to triadimenol than isolates collected from other cultivars. Throughout the experiments reported here cultivar \times fungicide interactions were seldom significant, and different fungicide treatments performed equally on all three cultivars. When first introduced Triumph hardly needed treatment with DMI fungicide because of effective host-plant mildew resistance and, as a result little fungicide selection pressure was applied to the small mildew populations on this cultivar. Triumph became very widely grown in England, and selection for mildew compatibility on this cultivar was strong. Eventually DMI fungicides were used to control mildew which appeared increasingly on this cultivar. As a result fungicide selection pressure increased on these emerging populations. The development of triadimenol resistance on independent occasions is also suggested by recent restriction fragment length polymorphism analysis of several barley mildew isolates (J.K.M. Brown, personal communication). Thus it seems unlikely that the spread of triadimenol resistance in barley powdery mildew can be combated through use of particular cultivars, as has so far proved effective in lettuce against the spread of phenylamide-resistant *Bremia lactucae* (Crute and Harrison, 1988).

These experiments have compared two entirely different assay techniques. The bait plant technique provides direct information from all field plots, even where mildew is difficult to detect, or where it no longer actively sporulates. The laboratory assay is less labour-intensive, but fails if insufficient inoculum is available from field plots. Although a few anomalies have occurred, the two assay procedures have, in general, identified similar changes in fungicide sensitivity in response to different fungicide strategies.

Acknowledgements

The authors wish to thank Bayer (UK) Ltd., and ICI Agrochemical Plc., for their interest and financial support for this work.

Samenvatting

Factoren die de opbouw van fungicideresistentie in meeldauw van zomergerst beïnvloeden

In veldexperimenten met herhalingen uitgevoerd in Engeland, gedurende een periode van 3 jaar in Avon en gedurende een periode van 2 jaar in Warwickshire, werd na behandeling van zomergerst met ethirimol of triadimenol een verminderde gevoeligheid van meeldauw voor deze fungiciden waargenomen.

Behandelingen met mengsels van ethirimol-triadimenol of tridemorf-triadimenol gaven weinig tot geen verminderde gevoeligheid. Verminderde gevoeligheid van isolaten voor ethirimol was meestal gecorreleerd met een verhoogde gevoeligheid voor triadimenol en omgekeerd. Vroeg in het seizoen werd in de meeldauwpopulatie op de

twee proefvelden een verschil in gevoeligheid voor de fungiciden waargenomen. Op één proefveld trad van het ene op het andere seizoen een aanzienlijke verandering in de gevoeligheid voor de fungiciden op. Er was geen duidelijke correlatie tussen de waargenomen verminderde gevoeligheid voor de fungiciden en de gebruikte cultivars of voorkomende fysio's. Verminderde gevoeligheid voor de fungiciden werd zowel bij zaadbehandeling als bij het bespuiten van planten waargenomen.

References

- Bolton, N.J.E. & Smith, J.M., 1988. Strategies to combat fungicide resistance in barley powdery mildew. Proceedings of the 1988 Brighton Crop Protection Conference – Pests and Diseases 1: 367-372.
- Brent, K.J., 1982. Case study 4: Powdery mildew of barley and cucumber. In: J. Dekker & S.G. Georgopoulos (Eds), Fungicide resistance in crop protection. PUDOC, Wageningen, p. 219-230.
- Butters, J.A., Clark, J. & Hollomon, D.W., 1983. Field evaluation of fungicide strategies to control barley powdery mildew. Proceedings of the 10th International Congress of Plant Protection 2: 644.
- Butters, J.A., Clark, J. & Hollomon, D.W., 1984. Resistance to inhibitors of sterol biosynthesis in barley powdery mildew. Mededelingen Faculteit Landbouwwetenschappen Rijksuniversiteit Gent 49: 143-151.
- Crute, I.R. & Harrison, J.M., 1988. Studies on the inheritance of resistance to metalaxyl in *Bremia lactucae* and on the stability and fitness of field isolates. Plant Pathology 37: 231-250.
- Fletcher, J.T. & Wolfe, M.S., 1981. Insensitivity of *Erysiphe graminis* f. sp. *hordei* to triadimefon, triadimenol and other fungicides. Proceedings of the 1981 British Crop Protection Conference 1: 51-58.
- Heaney, S.P., Martin, T.J. & Smith, J.M., 1988. Practical approaches to managing anti-resistance strategies with DMI fungicides. Proceedings of the 1988 Brighton Crop Protection Conference – Pests and Diseases 3: 1097-1107.
- Hoare, F.A., Hunter, T. & Jordan, V.W.J., 1986. Influence of spray programmes on development of fungicide resistance in the eyespot pathogen of wheat, *Pseudocercospora herpotrichoides*. Plant Pathology 35: 506-511.
- Hollomon, D.W., 1977. Laboratory evaluation of ethirimol. In: N.R. McFarlane (Ed.), Crop protection agents: their biological evaluation. Academic Press, London, p. 505-515.
- Hollomon, D.W., 1981. Genetic control of ethirimol resistance in a natural population of *Erysiphe graminis* f. sp. *hordei*. Phytopathology 71: 536-540.
- Hollomon, D.W., 1982. The effects of tridemorph on barley powdery mildew: its mode of action and cross sensitivity relationships. Phytopathologische Zeitschrift 105: 279-287.
- Hollomon, D.W., Butters, J.A. & Clark, J., 1984. Genetic control of triadimenol resistance in barley powdery mildew. Proceedings of the 1984 British Crop Protection Conference – Pests and Diseases 2: 477-482.
- Hollomon, D.W., Locke, T. & Proven, M., 1985. Sensitivity of *Erysiphe graminis* f. sp. *hordei* to ethirimol in relation to field performance. EPPO Bulletin 15: 467-471.
- Hunter, T., Brent, K.J. & Carter, G.A., 1984. Effects of fungicide regimes on sensitivity and control of barley mildew. Proceedings of the 1984 British Crop Protection Conference – Pests and Diseases: 471-476.
- Josepovits, G., 1989. A model for evaluating factors effecting the development of insensitivity to fungicides. Crop Protection 8: 106-113.
- Sanders, P.L., Houser, W.J., Parish, P.J. & Cole, H. Jr., 1985. Reduced rate fungicide mixtures to delay resistance and to control selected turf grass diseases. Plant Disease 69: 939-943.

- Shaw, M.W., 1989. A model of the evolution of polygenically controlled fungicide resistance. *Plant Pathology* 38: 44-55.
- Skylakakis, G., 1982. The development and use of models describing outbreaks of resistance to fungicides. *Crop Protection* 1: 249-262.
- Skylakakis, G., 1985. Two different processes for the selection of fungicide resistant subpopulations. *EPPO Bulletin* 15: 519-525.
- Staub, T. & Sozzi D., 1983. Recent practical experiments with fungicide resistance. *Proceedings of the 10th International Congress of Plant Protection* 2: 591-598.
- Wolfe, M.S. & Dinooor, A., 1973. The problems of fungicide tolerance in the field. *Proceedings of the 7th British Crop Protection Conference* 1: 11-19.
- Wolfe, M.S., Slater, S.E. & Minchin, P.N., 1983. Fungicide insensitivity and host pathogenicity in barley mildew. *Proceedings of the 10th International Congress of Plant Protection*: 645.